BEHAVIORAL BIOLOGY OF THE STRIPED GRASS LOOPER, *Mocis latipes* (Guenée), IN NORTH-CENTRAL FLORIDA

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1985

"For the things we have to learn before
we can do them, we learn by doing them."

Aristotle

ACKNOWLEDGEMENTS

I thank the members of my supervisory committee, Dr. D. H. Habeck, Dr. F. A. Johnson, and Dr. O. C. Ruelke for their unequivocal interest in my research program. The willingness with which each has so often set aside the demands placed on him from other quarters that he might assist me by kind word, field conference, thoughtful criticism, or procurement of temporary employment, has left me with a clearer perception of a teacher's proper role. To my mind, teacher is the most exalted of titles; upon them, it has indeed been fittingly bestowed.

I would be remiss if I did not here extend an indication of my gratitude to Dr. D. R. Minnick, for my graduate study's inception is largely a consequence of his supports, encouragements, and vision. I am deeply indebted.

I greatly appreciate the time and effort given by Bill Carpenter of the Entomology and Nematology Department and by Pat Carlysle of the USDA/ARS Laboratory; in large measure, the electron microscopy is their handiwork.

No mere word or fine sounding phrase can serve as ample requital for the forbearance so lovingly given by my wife Nancy. Without her, both my work and I are blank pages.

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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By

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August 1985

Chairman: Dr. D. H. Habeck
Major Department: Entomology and Nematology

A field population of adult *Mocis latipes* (Guenée), (Lepidoptera: Noctuidae) preferred to visit culms of bahiagrass, *Paspalum notatum* Flugge, rather than culms of either crabgrass, *Digitaria sanguinalis* (L.) Scop., or bermudagrass, *Cynodon dactylon* (L.) Pers. Nightly moth visitation peaked at ca. 20:00 hrs EDST and remained substantially unchanged for the next three hours.

In Callie giant bermudagrass, *C. dactylon*, adult *M. latipes* were more often observed to rest, mate and oviposit in stands of grass that possessed closed canopies. Moths usually deposited their eggs singly and demonstrated little

propensity to oviposit on any particular plant part. Oviposition occurred from 21:00 hrs to 22:30 hrs. In copulo pairs were sessile, highly visible, and usually found in upper portions of bermudagrass canopy. Mating activity peaked at 01:00 hrs, but occurred from 21:00 hrs to 04:00 hrs.

Larval activity was nocturnal. Fifth and sixth instar larvae ascended from and returned to basal portions of bermudagrass canopy about an hour earlier than third and fourth instars. Vertical movement was most pronounced from 19:00 hrs to 21:00 hrs and from 06:00 hrs to 08:00 hrs.

Mark-release-recapture evaluations of a pushcart sampling device indicated a low, but consistent, proportion of third and fourth instar M. latipes larvae present in Callie giant bermudagrass may be recaptured when the device is employed at either 20:00 hrs or 07:00 hrs. Of these two times, sampler efficiency was higher at 20:00 hrs.

Following hatch, M. latipes larvae consumed more than one-half of the chorion's spheroidal portion.

In petri dish culture, both first and second instar M. latipes larvae chose to feed only on upper surfaces of Callie giant bermudagrass blades. Scanning electron microscopy revealed tooth-like trichomes were more abundant on blade margins and lower surfaces than on upper surfaces.

Stage-specific developmental times for M. latipes larvae reared in the laboratory on Callie giant bermudagrass foliage were comparable to those that have been reported

when other grasses were supplied as diet. The average pupal mass that resulted from larvae having been reared on Callie giant bermudagrass was noticeably greater than values previously reported for other diets.

INTRODUCTION

Of the four Mocis spp. known to occur in Florida (Ogunwolu and Habeck 1979), the striped grass looper, Mocis latipes (Guenée), (Lepidoptera: Noctuidae), is the species most likely to achieve economically injurious population levels in North-Central Florida fields planted to forage grasses (Genung and Allen 1974). Although dynamics of the market price for hay and production overhead coupled with both species and cultivar-specific differentials in harvestable grass growth necessitates a virtual case-by-case definition of "injurious level", some indication is given by noting that M. latipes larval populations evincing densities from 3 to 8 larvae per m^2 have been adjudged detrimental (Reinert 1975).

M. latipes is present in Florida throughout the year (Kimball 1965); however, from Lake Okeechobee northward, population levels are usually low prior to July or August. Thereafter, larval populations may remain high until early December (Genung and Allen 1974) or until cold weather checks the growth of warm-season grasses (which, for the Gainesville region, can be expected in mid-November).

Although considerable variation may be evidenced in a series of specimens (Forbes 1960), the imago is usually grey-brown with a wingspan of about 4 cm. The mesothoracic

wings possess strong antemedial and postmedial lines, with the latter being only slightly inflected as it approaches the anal margin. The reniform is usually visible, but may be obscure; and the subreniform is a fine, fully-closed, near-perfect circle, a portion of which is contiguous (or nearly so) with the postmedial line. Moth gender is easily ascertained: a profuse growth of clothing setae on the metathoracic tibiae is present on males but not females.

M. latipes larvae possess longitudinal stripes that extend from the adfrontal area to the the anal prolegs; their coloration is highly variable (Ogunwolu 1974). Since ventral prolegs are present only on the fifth and sixth abdominal segments, larval gait is similiar to that of the measuring worms; from whence comes the common name, striped grass looper.

Viewed cumulatively, a considerable body of literature has been put forward and substantial progress made toward gaining a better understanding of various aspects of M. latipes' biology, taxonomic position, and pest status; however, our knowledge of this moth's behavior in North-Central Florida grasslands has long been in need of enrichment. Recent advances in the development of high-yielding forage grass varieties for this region make this need both more evident and urgent; for many of the more promising varieties achieve peak growth during the part of the year that M. latipes can be most expected to achieve economically injurious populational levels (Ruelke 1983).

Without an understanding of how the adults and larvae of M. latipes behave in both field and plant space, through time, in the presence of multiple grass species, and on agriculturally-important grass varieties, efforts directed toward their populations' management that utilize either monitoring or sampling methodologies in a predictive capacity are likely to provide less than optimal results.

This belief is the foundation of the studies here presented. These include examination of

1. the relationship between time of night and moth visitation to three of M. latipes' known host plants;

2. the influence of grass age on, and degree of time specificity for: nightly moth abundance, oviposition, and mating behavior of M. latipes in Callie giant bermudagrass;

3. the times for which different ages of M. latipes larvae change their location in Callie giant bermudagrass canopy;

4. the potential usefulness of a new grassland sampling device as a tool for making absolute density estimates of third and fourth instar M. latipes larvae in Callie giant bermudagrass;

5. the proportion of the chorion that first instar M. latipes larvae consume during the post-eclosion period;

6. the degree of specificity evidenced by first and second instar M. latipes larvae for feeding on either upper or lower surfaces of Callie giant bermudagrass blades; and

7. the stage-specific developmental schedule that results when M. latipes larvae are supplied ad libitum quantities of Callie giant bermudagrass foliage.

LITERATURE REVIEW

The literature treating the striped grass looper, Mocis latipes (Guenée), (Lepidoptera: Noctuidae: Catocalinae) spans 133 years, encompasses 2 continents, and mirrors this moth's believed geographical range.

After examining 28 specimens, Guenée (1852) placed this species in the genus Remigia; hence, several entomological authors of the 19th century refer to this moth as R. latipes Guenée (Bethune 1869; Moschler 1880, 1886; Gundlach 1881; Smith 1893; and Swainson 1900). During this era, this species was incorrectly accorded a position in various other noctuid genera; notably, Noctua and Ophiusa (Hampson 1913) and Pelamia, Baratha, and Cauninda (Hodges et al. 1983). The systematic revision by Hampson (1913) is the earliest reference placing this moth in the genus Mocis; however, broad acceptance seems to have been delayed for at least a decade following Hampson's efforts. Perhaps as the final holdout, Bissell (1940) refers to this insect as Pelamia latipes Guenée.

Synonymy at the species level has served to exacerbate the consternation that expectedly accompanies confusion of genera. In the past, the moth now recognized as M. latipes has been designated by a variety of specific epithets; these

include: repanda, punctularis, deliquens, excidens, subtilis, convieniens, collata, detersa, indentata, and difluens (Hampson 1913). The vast majority of these names convey little real difficulty; they are principally the result of Walker's work at the British Museum and have been resolved since the early part of the 20th century (Hampson 1913). That so many names have been applied to a single species is evidence of both the difficulties inherent in the taxonomy of this group and the intra-species diversity of M. latipes. Passoa (1983) points this out, and Forbes (1960) clearly enunciates the differences in forewing markings most often seen in a series of specimens of this highly variable species. Regarding synonymy, the most enduring difficulty is the use of repanda, which is (in correct application) the epithet of a sibling species described by Fabricius in 1794 and has been misapplied as an epithet in synonomy with latipes (Hodges et al. 1983).

Notwithstanding the early and pointed indications by Gundlach (1881), Moschler (1880, 1886), and Smith (1893) that Remigia repanda and Remigia latipes were different species, the epithet repanda has been a chronic synonym for latipes (Dyar 1902, Vickery 1924, Watson 1933, Wolcott and Otero 1936, Labrador 1964). The opening statement in Kimball's (1965) treatment of Mocis in Florida is a cautionary note that ". . . many of the records may be mixed . . . ." (Kimball 1965, p. 125); and, when reporting on M. latipes, he states: ". . . confusion has arisen

because the species at one time went under the name Remigia repanda (Fabricius) . . . ." (Kimball 1965, p. 125). All of the literature from the United States that mentions Mocis (=Remigia) repanda is, in fact, treating M. latipes; for M. repanda (F.) is not known to occur in this country (Hodges et al. 1983). Unfortunately, no such clear-cut aid is available for separating the Central and South American literature.

In addition to describing the imago, Guenée (1852) provided the first descriptions of M. latipes larvae and pupae. Others that have given larval descriptions include Dyar (1900), Swainson (1900), Jones and Wolcott (1922), Crumb (1956), Forbes (1960), and Labrador (1964). None of these works prove sufficient for species-specific determinations of either larval or pupal specimens; this inadequacy has been addressed by Ogunwolu and Habeck (1979).

The particulars of M. latipes' geographical origin remain an enigma; past efforts of systematists seem to suggest (by tacit agreement) that this moth is a native of the tropical regions (Hampson 1913, Schaus 1940, Forbes 1960, Hodges et al. 1983). Guenée (1852) states that his specimens were secured from widely separated locales, and included Labrador and Madagascar. He maintained that M. latipes occurs throughout central Africa and in both North and South America, a notion with which Hampson (1913) was in complete accord. Schaus (1940) pointed out that the genitalia of the American specimens differed from those of

African specimens, and suggested that the American moths were a distinct species.

Holland reported that M. latipes' range extends from northern Canada to Argentina and that the moth keeps to the eastern side of both the Rocky and Andes Mountains (Holland 1920); subsequent workers concur (Vickery 1924, Forbes 1960, Reinert 1975). This moth's presence in the cooler regions of its known range is quite probably the consequence of a seasonally-mediated dispersal; Forbes has described this species as one that obtains the limits of its range by ". . . straggling northward to Canada in the Fall . . ." (Forbes 1960, p. 344), thereby offering a possible means of accounting for Bethune (1869) being able to secure 2 specimens of M. latipes from the northern shore of Lake Ontario.

For the past 60 years, the reports and investigations of M. latipes' occurrence in the United States have been confined to the states of the southeastern region. These include: Texas (Vickery 1924), Alabama (Blake et al. 1959, Guyton 1959), South Carolina (Anonymous 1961, Cuthbert 1954, Nettles 1954), Georgia (Anonymous 1954; Bissell 1940; Beck 1955; Benton and Beck 1957; Dupree 1959; Geiger 1954; Johnson 1957, 1959a, 1959b; Johnson and Buchanan 1957; Jordan 1954, 1959; McGill 1957; Morgan 1955), and Florida (Anonymous 1961, 1972, 1975a, 1975b; Beem 1954; Brinkley 1954; Clinton and Shirar 1965; Denmark 1957; Genung 1964, 1966, 1967, 1968, 1971; Genung et al. 1976; Jones and Hodges

1953; Jones et al. 1952; Kelscheimer 1952, Kelsheimer et al. 1953; Kimball 1965; Kleyla et al. 1979; Koehler et al. 1977; Kuitert 1954; Maltby 1954; May 1954; Mead 1965, 1970; Ogunwolu 1974; Ogunwolu and Habeck 1975, 1979; Reinert 1975; Strayer 1971; Van Pelt 1954a, 1954b; Ware 1973; Watson 1933; Wolfenbarger 1955).

M. latipes has long been recognized as an injurious species in the Caribbean. Contributions to the literature have been made from Cuba (Babayan et al. 1975, Gundlach 1881), Jamaica (Moschler 1886), Puerto Rico (Capriles and Ferrer 1973; Jones and Wolcott 1922; Van Dine 1913; Wolcott 1921, 1923, 1948; Wolcott and Martorell 1943, Wolcott and Otero 1936), Trinidad (Mahadeo 1977, Urich 1910), and, the Windward and Leeward Islands (Fennah 1947).

Surprisingly little literature is available from the Central American mainland; however, McGuire and Crandall (1967) have reported that M. latipes is present as a pest of agricultural commodities in Mexico, Guatemala, Costa Rica, El Salvador, Honduras, Nicaragua, and Panama. Passoa (1983) has confirmed that this moth adversely affects agriculture in Honduras.

In the past several decades, a considerable body of literature treating various aspects of M. latipes has emerged from some of the South American countries, notably, Colombia (Varela and Calderon 1982), Guyana (Bodkin 1914, Rambajan 1981), Surinam (Moschler 1880, Van Dinther 1971), Venezuela (Labrador 1964), Bolivia (Munro 1960), Brazil

(Bastos et al. 1979; Cruz and Santos 1983; Ferreira and Parra 1984a, 1984b; Hseih 1979; Lara et al. 1977; Lara and Silviera Neto 1977; Lima and Berti Filho 1984; Lourencao et al. 1982), Argentina (Costilla et al. 1973, Hayward 1960), and Uruguay (Biezanko et al. 1957).

Much has been learned about M. latipes' life history and biology. In his discussion of the larvae, Guenée (1852) informs us that these, ". . . s'enterre vers le commencement d'aout . . . ."; and, regarding the imago, ". . . se trouve à la fin d'aout . . ." (Guenée 1852, p. 315). Hence, he [Guenée] provides the first record of this species' seasonal presence [August] and an approximation of its life cycle's duration [about 1 month]. Dyar (1900) reared Mocis larvae and briefly mentioned their nocturnal habits. Urich (1910) noted that Mocis larvae were found singly on grass blades, and that they dropped to the soil's surface at the slightest disturbance. Jones (1913) distinguished M. latipes larval damage from that caused by Spodoptera frugiperda Smith by noting that larvae of the former fed on unfolded sugarcane leaves, whereas larvae of the latter fed in the plant's whorl. After viewing the damage caused by M. latipes in Texas grasslands, Vickery (1924) conducted the first detailed lab studies of this moth's biology, subsequently determining that the larvae were not cannibalistic and could be readily reared on leaves of Zea mays L. He found that the eggs are deposited singly, that development from egg to pupa required 21 days, and that the pupal stage

had an average duration of 12 days (Vickery 1924). Reporting from the Antilles, Fennah (1947) declared himself in agreement with Vickery insofar as larval developmental time was concerned, but noted that pupal duration was only 6 days. In reporting M. latipes' clutch size, Fennah is virtually alone, stating that, ". . . eggs are laid on the leaves in clusters of 40 - 60 close to the midrib below the leaf, . . ." (Fennah 1947, p. 86); only Van Dinther (1954) has voiced similiar findings, maintaining that clutch size is as large as 8 ova per ovipositional site.

Labrador (1964) found that a typical female produced an average of 182 eggs in her lifetime, and that eclosion from the egg required a 3 or 5 day incubation at 25° C or 28° C, respectively; larval and pupal developmental times were in agreement with those given by Vickery. Labrador also measured the adult's lifespan, finding that moths fed a dilute solution of honey would live from 2 to 17 days, with the average being 9 days (Labrador 1964). Ogunwolu (1974) measured the adult longevity of field-caged moths and found that these will live an average of 11 days. Ogunwolu and Habeck (1975) reported that M. latipes adults kept in cardboard containers and fed a 10% sucrose solution produced 94 to 458 eggs per female, and that under these conditions, the average number of fertile eggs was 277.4 (Ogunwolu and Habeck 1975). In sharp contrast, the Cuban research team of Babayan et al. (1975) reported that M. latipes adults provided a sucrose solution lived up to 49 days and produced

from 215 to 611 eggs per female, with the average number of eggs being 407.1. They report the larval developmental time as being from 22 to 75 days (Babayan et al. 1975).

Studies of M. latipes reared in environmentally-regulated growth chambers have been conducted by Ferreira and Parra (1984a); these researchers detected no significant differences in larval developmental time when temperature is regulated to 20°, 25° or 30° C; but that temperatures of 35° C or higher produce adverse effects. They conclude that M. latipes has a developmental threshold of 13.7° C, and that at this temperature, this species requires 391.30 growth-degrees to develop from egg to adult (Ferreira and Parra 1984a). They also investigated the effects of photoperiod on laboratory-reared M. latipes larvae, and found that larvae reared under a 14:10 (light:dark) regimen yielded pupae that were significantly different in mass from those produced from larvae reared under either 10:14 or 12:12 (Ferreira and Parra 1984b).

Reinert (1975) fed M. latipes larvae freshly-cut terminal stolons of St. Augustinegrass, Stenotaphrum secundatum (Walt.) Kuntz, and noted that these larvae, ". . . consumed an average of 442.44 mg of leaf tissue during their development with an average conversion ratio of 0.25 . . . ." (Reinert 1975, p. 203). He contends that larval efficiency in converting leaf tissue to body tissue is greatest in the penultimate larval instar (Reinert 1975). Conducting investigations in a similiar vein, Ogunwolu and

Habeck (1975) noted that of the grass species which they evaluated, M. latipes larvae both took longer to develop and had higher early-instar mortality rates when confined to a St. Augustinegrass diet. They also evaluated larval performance on non-grass hosts and found that, without exception, M. latipes larvae die without feeding when provided a diet of only legume foliage; and that, when given the choice of both legumes and grasses, the larvae feed only upon the latter (Ogunwolu and Habeck 1975). More recently, Cruz and Santos (1983) have determined M. latipes larvae demonstrate no significant differences in developmental time, pupal mass, or larval mortality, when reared on foliage of either corn, Zea mays L., or Johnsongrass, Sorghum halepense (L.) Pers.; they report observing a 55% mortality rate in larvae fed an artificial diet (Cruz and Santos 1983).

Very little of the literature on M. latipes treats the subjects of populational dynamics or moth behavior in the field. Silviera Neto et al. (1977) have investigated the flight activity time of this moth species in Brazil and report that in an automatic light trap calibrated to partition nightly catches into 3-hour units, M. latipes is taken only during the intervals of 18:00-21:00 hours and 21:00-24:00 hours; moreover, moth abundance in the early evening interval is about twice that obtained for the late night interval. Lara and Silviera Neto (1977) analyzed light trap catches for the interval July 1972 to June 1975

and concluded that in Jaboticabal, Brazil M. latipes is present year-round, and that its populational presence is bimodal with peaks occurring during the months of June and December. Also reporting from Brazil, the team of Lara et al. (1977) studied M. latipes' presence in different locales and developed a predictive index, ". . . índice Constancia Simultanea . . ." (Lara et al. 1977, p. 52), with which they demonstrate capture of a M. latipes adult in one locale is sufficient to predict its presence in another.

Although most have not made M. latipes' seasonal presence the focal point of their efforts, numerous authors have mentioned the time of year pertinent to their observations. In general, these are indicative of populations that have caused serious injury to some crop. Such remarks are scattered widely through the literature; however, in composite, these serve to provide a fairly clear picture of this moth's seasonal presence in various latitudes of the Western Hemisphere; e.g., Argentina: Feb., Mar. (Costilla et al. 1973); Uruguay: Feb., Mar., Apr. (Biezanko et al. 1957); Brazil: Jan., Feb. (Lourencao et al. 1982); the Amazon Basin of Brazil: Apr., May (Hseih 1979); Colombia: Sept. (Alvarez and Sanchez 1981); Venezuela: Oct. (Labrador 1964); British Guiana: year-round (Bodkin 1914); Guyana: year-round (Rambajan 1981); Trinidad: Feb., Mar., Apr. (Urich 1910), Aug. (Mahadeo 1977); Panama: Sep., Oct. (Crumb 1956); Honduras: Mar., Jun., Jul., Aug., Nov. (Passoa 1983); Puerto Rico: year-round (Jones 1913; Wolcott 1921, 1948; Wolcott

and Martorell 1943; Wolcott and Otero 1936; Capriles and Ferrer 1973); Cuba: Sep. (Babayan et al. 1975); Florida: year-round (Kimball 1965); Texas: Oct. (Vickery 1924); Alabama: Oct. (Blake et al. 1959, Guyton 1959); Georgia: Mar., (Johnson 1957); Aug., Sep., Oct. (McGill 1957, Morgan 1955, Geiger 1954); and, South Carolina: Sep., Oct. (Nettles 1954, Cuthbert 1954).

Many authors that have contributed to the literature on M. latipes have included in their remarks some treatment of this insect's host plants. In several cases these remarks have been of a general nature, citing M. latipes on some undetermined grass, pasture plant, or cover crop (Anon. 1954, Cuthbert 1954, Denmark 1957, May 1954, Passoa 1983, Swainson 1900, Wolfenbarger 1955). A few authors, notably Vickery (1924), Labrador (1964), and Tietz (1972), have iterated the findings of others (and thus to a greater or lesser extent have provided a host plant list). Most authors have reported M. latipes only on the plant (or plants) of immediate interest in their studies; in consequence, reports of the host plants of M. latipes are scattered widely throughout the literature. In composite, these reports provide a reasonably clear picture of this insect's hosts and indicate that many of the agriculturally important grasses serve in this capacity. These include: sugarcane, Saccharum officinarum L., (Biezanko et al. 1957; Capriles and Ferrer 1973; Costilla et al. 1973; Hayward 1960; Holloway 1933; Jones 1913; Jones and Wolcott 1922; Labrador

1964; Mahadeo 1977; Tietz 1972; Urich 1910; Van Dine 1913; Vickery 1924; Wolcott 1921, 1948; Wolcott and Martorell 1943); bermudagrass, Cynodon dactylon (L.) Pers., (Anon. 1973, 1975a, 1975b; Beck 1955; Costilla et al. 1973; Geiger 1954; Johnson 1957, 1959a; Johnson and Buchanan 1957; Morgan 1955; Labrador 1964; Ogunwolu and Habeck 1975; Vickery 1924; Watson 1933); corn, Zea mays L., (Biezanko et al. 1957, Cruz and Santos 1983, Costilla et al. 1973, Hayward 1960, Kimball 1965, Labrador 1964, McGill 1957, Passoa 1983, Tietz 1972, and Vickery 1924); rice, Oryza sativa L., (Biezanko et al. 1957, Hayward 1960, Hseih 1979, Kimball 1965, Labrador 1964, Munro 1960, Passoa 1983, Rambajan 1981, Van Dinther 1971); millet, Pennisetum americanum L., (Benton and Beck 1957, Blake et al. 1959, Johnson 1959b, McGill 1957, Ogunwolu and Habeck 1975); bahiagrass, Paspalum notatum Flugge, (Anon. 1972, Beck 1955, Brinkley 1954, Lourencao et al. 1982, Ogunwolu and Habeck 1975, Van Dinther 1971, Van Pelt 1954b); Pangola digitgrass, Digitaria decumbens Stent., (Costilla et al. 1973, Genung 1971, Jones et al. 1952, Jones and Hodges 1953, Kelsheimer et al. 1953, Kuitert 1954, Maltby 1954); guineagrass, Panicum maximum L., (Capriles and Ferrer 1973, Labrador 1964, Lourencao et al. 1982, Urich 1910, Wolcott 1948); paragrass, Brachiaria mutica (Forsk.) Stapf., (Kelsheimer et al. 1953, Genung 1968, Labrador 1964, Urich 1910); hairy crabgrass, Digitaria sanguinalis (L.) Scop., (McGill 1957, Tietz 1972, Watson 1933); Saint Augustine-grass, Stenotaphrum secundatum (Walt.) Kuntz, (Anon. 1972,

Genung 1966, Ogunwolu and Habeck 1975, Reinert 1974); sudangrass, Sorghum sudanense (Piper) Stapf., (Genung 1964, McGill 1957, Ogunwolu and Habeck 1975); grain sorghum, Sorghum bicolor (L.) Moench, (Costilla et al. 1973, Labrador 1964); wheat, Triticum aestivum L., (Biezanko et al. 1957, Labrador 1964); oats, Avena sativa L., (Jordan 1954, Mead 1965); maidencane, Panicum hemitomon Schult., (Clinton and Shirar 1965); jaraguagrass, Hyparrhenia rufa (Stapf.), (Labrador 1964, Lourencao et al. 1982); dallisgrass, Paspalum dilatatum Poir., (Dupree 1959); ryegrass, Lolium multiflorum Lam., (Genung 1967); Salina buffelgrass, Cenchrus ciliaris L., (Capriles and Ferrer 1973); Napiergrass, Pennisetum purpureum Schumach., (Costilla et al. 1973, Wolcott 1948); Johnsongrass, Sorghum halepense (L.) Pers., (Cruz and Santos 1983); Transvala digitgrass, Digitaria decumbens Stent., (Ogunwolu and Habeck 1975); goosegrass, Elusine indica (L.) Gaertn., (Labrador 1964); dogtoothgrass, Cynodon incompletus Nees., (Ogunwolu and Habeck 1975); rhodesgrass, Chloris gayana Kunth, (Ogunwolu and Habeck 1975); multiflowered false rhodesgrass, Trichloris pluriflora Fourn., (Tietz 1972, Vickery 1924); malojillograss, Panicum barbinode L., (Jones 1913); carimaguagrass, Andropogon gayanus L., (Varela and Calderon 1982); and, natalgrass, Tricholaena rosea Nees., (Watson 1933). M. latipes has also been reported by Labrador (1964), Tietz (1972) and Vickery (1924) on several grasses which lack common names. These include: Eriochloa punctata

L., Leptochloa neallyi Vasey, Cenchrus viridis Spreng., Cenchrus brownii Roem., Panicum faciculatum Swartz, Paspalum faciculatum Wihl., and Ioxphorus unisetus L. In his original description of the moth, Guenée (1852) noted that M. latipes larvae fed on blades of Hypericum sp.

In addition to the aforementioned 39 grasses, M. latipes has been periodically reported to occur on various non-grasses, including: alfalfa, Medicago sativa L., (Kleyla et al. 1979, Labrador 1964, Jordan 1959, Costilla et al., 1973); soybean, Glycine max (L.) Merr., (Bissell 1940, Costilla et al., 1973); field pea, Pisum sativum L., (Labrador 1964, Van Pelt 1954a); beans, Phaseolus vulgaris L., (Biezanko et al., 1957); cowpea, Vigna sinensis (Endl.), (Hayward 1960); hairy indigo, Indigofera hirsuta L., (Beem 1954); broadbean, Vicia faba L., (Kimball 1965); sweet potato, Ipomoea batatas (L.) Lam., (Guyton 1959); turnip, Brassica campestris L., (Kimball 1965); coffee, Coffea arabica L., (Labrador 1964); and, Washington palm, Washingtonia robusta Wendl., (Ware 1973).

Reports of non-grass host plants of M. latipes have evoked protestation by some researchers. After noting that most of these non-grasses are members of the Leguminosae, Ogunwolu and Habeck (1975) undertook to rear M. latipes larvae on leaf tissue of several different legume species; their findings led them to conclude that reports of M. latipes on non-grasses are probably erroneous if the determinative criterion of a host plant includes larval

development. It seems quite possible that reports of non-grass hosts of M. latipes have been the consequence of a researcher having observed last-instar larvae seeking a pupation site, or the finding of M. latipes pupae on a non-grass plant. Wolcott (1948) has reported finding M. latipes pupae on Ipomoea sp. and Lourencao et al. (1982) have noted that M. latipes pupae can be found on Bidens pilosa L. foliage. Similiarly, Ogunwolu and Habeck (1975) have recorded collecting M. latipes pupae from blackberry, Rubus cuneifolius Pursh; dogfennel, Eupatorium compositifolium Walt.; ragweed, Ambrosia artemisifolia L.; and Florida pusley, Richardia scabra L.

The earliest mention of natural enemies of M. latipes is probably that of Urich (1910), who observed that the savannah black bird, Quiscaulus crassirostris Swainson, and the smooth-billed ani, Crotophaga ani L., would feed on M. latipes larvae that had been dislodged from sugarcane foliage by laborers busy weeding the fields. Urich also mentioned that, ". . . a number of parasitical flies were bred from the caterpillars taken from the fields . . . ." (Urich 1910, p. 161); however, he made no specific determination of the parasites. Shortly thereafter, Bodkin (1914) reported the coccinellid, Megilla maculata DeGeer, and the Demerara robin, Leistes guianensis L., as predators of M. latipes larvae. Jones and Wolcott (1922) noted that, in Puerto Rico, 90% of the parasitization of M. latipes larvae could be attributed to three species of tachinid flies:

Phorocera claripennis Macq., Linnaemyia fulvicauda Walton, and Helicobia helicis Townsend. In addition, they recorded the chalcid, Chalcis robusta Cresson; the sarcophagid, Sarcophaga sternodontis Townsend; and an ichneumonid, Rogas sp., as parasites of this moth's larvae (Jones and Wolcott 1922). However, Vickery (1924) reported examining large numbers of Mocis larvae and pupae in Texas but was unable to rear any parasites from them. Vickery found a single larva parasitized by Euplectrus sp., but stated that the parasites died as immatures (Vickery 1924). Fennah (1947) confirmed the findings of predecessors and added Sarcophaga lambens Wd. to the list of parasites reared from M. latipes; and, Wolcott (1948) cited the lizards Anolis cristatellus Duméril and Bibron, Anolis krugii Peters, Anolis pulchellus Duméril and Bibron, and Anolis stratulus Cope as predators. After conducting crop-content analyses, Genung and Greene (1974) and Genung et al. (1976) concluded that both the eastern meadowlark, Sturnella magna argutulla Bangs., and Maynard's redwing blackbird, Agelaius phoeniceus floridanus Maynard, are instrumental in reducing populations of M. latipes larvae in South Florida grasslands. Similiarly, Hodges et al. (1975) have noted the beneficial effects of blackbirds in Florida pastures.

To date, the most complete account of M. latipes natural enemies in North America comes from Ogunwolu and Habeck (1975); these researchers evaluated 325 Mocis pupae and found 6% of them parasitized. Parasites which they were

successful in rearing included the sarcophagids Sarcophaga sp. and Sarcodexia sternodontis Townsend; the braconids Apanteles scitulus Riley, Meteorus autographe Muesebeck, and Microplitis maturus Weed; the chalcids Brachymeria ovata ovata (Say) and Brachymeria robusta (Cresson); and the ichneumonids Coccygomimus aequalis (Provancher), Enicospilus purgatus (Say), Enicospilus arcuatus? (Felt), and Gambus ultimus (Cresson). They also reported that a tenebrionid adult, Bothrothes fortis (Casey), and a carabid larva, Pinacodera sp., prey on Mocis larvae (Ogunwolu and Habeck 1975). Babayan et al. (1975) mention having reared Euplectromorpha sp., Euplectrus sp., Brachymeria sp., Bracon sp., and Enicospilus sp. from M. latipes immatures. In sharp contrast to the findings of virtually all other researchers, this Cuban team reported parasitism levels in field-collected M. latipes larvae and pupae to be as high as 78% (Babayan et al. 1975).

Working in Venezuela, Labrador (1964) compiled a list of 27 arthropod parasites and predators of M. latipes. These include the sarcophagids Sarcodexia stenodontis Townsend, Sarcophaga aurea Hall, and Sarcophaga sp.; the tachinids Linnaemya fulvicuada Walt., Phorocera rusti Aldr., Helicobia helices Townsend, Achaetoneura aletiae Riley, Achaetoneura archippivora Will., Archytas marmoratus Townsend, Blondelia barmigera Coq., Cyrtophoeba sp., Euphorocera claripennis Macq., and Winthemia sp.; the exoristid Platelloapis sp.; the braconids Rogas sp. and Bracon sp.; the encyrtids

Copidosoma truncatellum Dalhm and Lytopilus sp.; the ichneumonids Ophion sp. and Enicospilus sp.; the chalcids Brachymeria incerta Cresson, Brachymeria robusta Cresson, Chalcis sp., and Spilochalcis femorata Fabr.; the carabid Calosoma alternans Fabr.; the vespid Polistes versicolor Oliv.; and, the sphecid Sceliphrons figulum Fahlb. (Labrador 1964).

Other natural enemies of M. latipes in South America include the tachinids Patelloa similis (Townsend), and Euphorocera floridensis Townsend; the ichneumonid Netelia sp.; and the vespid Polistes canadensis Hayward (Lourencao et al. 1982). Most recently, the eulophid Horismenus distinguendus Blanchard has been found to be capable of comleting its life cycle in the laboratory when provided with M. latipes pupae (Lima and Berti Filho 1984).

The natural enemies of M. latipes have not always effectively suppressed caterpillar-induced crop damage. In result, various corrective actions have been recommended or undertaken over the years. A few of these fall under the general category of cultural control and include such measures as flooding rice nursery plantings or burning infested pasturelands after the larvae have pupated (Bodkin 1914). Early researchers advocated using inorganic compounds such as lead arsenate, copper acetoarsenite, slaked lime, and sodium fluosilicate to control M. latipes larvae (Bodkin 1914, Jones and Wolcott 1922, Holloway 1933, Fennah 1947).

Immediately following World War II, several synthetic organic pesticides became relatively inexpensive and widely available; such compounds became the focus of a number of researchers interested in the chemical control of M. latipes in Florida pastures. Jones et al. (1952) noted that M. latipes larvae became paralyzed approximately 48 hours after an application of either DDT or chlordane, and that the same effect could be achieved within 24 hours by an application of toxaphene. An application of DDT, formulated as a 5% dust and distributed by towing a commercial fertilizer spreader set to deliver 30-35 pounds of dust per acre, was reported to control M. latipes larvae in a paragrass, B. mutica, pasture (Kelsheimer 1952, Kelsheimer et al. 1953). Although DDT has not been used in Florida pasture for nearly two decades, it is quite likely still used in other parts of the world; DDT was last cited as a material with which to control M. latipes by the Colombian research team of Costilla et al. (1973).

Jones and Hodges (1953) demonstrated that a spray made from parathion 15% wettable powder and applied at a rate of 0.75 pounds active ingredient per acre was sufficient to kill M. latipes larvae in Pangola digitgrass, D. decumbens. Labrador (1964) noted that either 0.25 kg carbaryl, 0.20 kg trichlorfon, or 0.50 kg toxaphene per 100 liters of water would control M. latipes larvae in a hectare of Venezuelan pasture. Strayer (1971) recommended carbaryl (either as a 5% dust or 80% sprayable), toxaphene (as a 10%

dust or 40% wettable powder), phosdrin (as a 2% dust or 25% emulsifiable concentrate), and parathion (as a 2% dust or 15% wettable powder) for control of M. latipes in Florida pastures. Koehler et al. (1977) concluded that a single aerial application of permethrin , applied at a rate of 0.2 pounds active ingredient per acre , will kill at least 84% of the M. latipes larvae in bermudagrass, C. dactylon, within 24 hours and virtually 100% within 72 hours.

Many authors have remarked that M. latipes may be a serious impediment to the production of some commodity, and in several instances, graphic accounts of M. latipes' destructiveness have been published (Bodkin 1914, Holloway 1933, Labrador 1964, Capriles and Ferrer 1973). However, very few documents provide any comparative measure of this insect's impact. McGuire and Crandall (1967) developed a ranking system for the economically injurious pests of select food crops produced in Central America. They ranked M. latipes as the 5th most important pest of corn, Z. mays; the 2nd most important pest of grain sorghum, S. bicolor; the 6th most important in rice, O. sativa; and, the premier pest of pasture grasses (McGuire and Crandall 1967). Martin et al. (1982) reported that M. latipes inflicted ca. $2.6 million damage to the hay and pasture industry in Georgia during the 1980 growing season.

MATERIALS AND METHODS

Field Experiments

Moth Attraction to Different Host Grasses

During the nights of 21-25 September 1983, the attraction of a field population of adult M. latipes to 1280 sample units was evaluated. Each sample unit contained 10 culms of a treatment grass or was a poultry wire control. The treatment grasses were: bahiagrass, P. notatum; hairy crabgrass, D. sanguinalis; and Callie giant bermudagrass, C. dactylon. Both the bahiagrass and the crabgrass culms had racemes; the bermudagrass culms were vegetative. All of the plant material used in the experiment was obtained from roadsides and fields of the University of Florida Campus Agronomy Farm; the experiment was conducted in one of its fields. Hourly measurements of temperature, rainfall, and relative humidity during the experimental interval were obtained from the Agronomy Farm weather data facility.

Forty receptacles were constructed; each was formed by cementing the base of a 7-dram plastic shell vial to the center of a 20 cm plastic potting saucer's inner surface. Ten receptacles were fitted with a 12 cm x 45 cm strip of 2.5 cm mesh poultry wire. These 10 receptacles were used as controls. The other 30 receptacles were partitioned

into three equal groups. The receptacles in each group were subsequently filled with culms of a given treatment grass.

On each afternoon preceding a nightly assay, 125 freshly-cut culms of each grass were collected, sealed in plastic bags, and transported to the experimental site. Culms of each grass were arbitrarily selected from the bags and their basal portions trimmed until all were ca. 45 cm long. These were grouped, species-specifically, to form 30 bundles of 10 culms. The base of each bundle was wrapped with a 2.5 cm x 12 cm strip of water-soaked surgical cotton and placed in a receptacle's water-filled shell vial.

At ca. 18:30 hrs, all receptacles were placed in the field and arranged in 1 row of 10 blocks. Each block measured 1 m per side and was 5 m from adjacent blocks. Every block contained all 3 treatment grasses plus a control. Random numbers determined the placement of receptacles in the corners of each block.

Once ever hour, from 19:00 hrs to 03:00 hrs, each block was visited and the number of M. latipes adults resting on the contents of each receptacle was recorded. Whenever a moth was seen, its behavior was noted and the resting site examined for clues of its attractiveness. A clear-lensed, 6-volt, headlamp fitted with a duct tape visor was used to aid observations.

Data were analyzed for differences in the total number of moths attracted to each of the grasses and for differences in average moth abundance per grass at the various

times of night. All tests for significance and confidence interval constructions were at the ($\alpha = 0.05$) level.

Moth Activity in Callie Giant Bermudagrass

On 30 June 1983, a 0.11 ha field with an established stand of Callie giant bermudagrass was chop-harvested to a stubble of ca. 12 cm and fertilized with 18 kg of a 17-5-10 (N-P_2O_5-K_2O) complete fertilizer. After 24 days of regrowth, the field was divided into 18 plots. Each plot measured 4 m x 12 m and was separated from adjacent plots by a 75 cm width of mowed alleyway. A random numbers table was used to designate both a harvest date for each plot and each plot's field location. Plot harvests were conducted on 1 August, 10 August, and 24 August. On each of the harvest dates, 6 plots were mowed with a garden-tractor-powered sickle bar set for a stubble height of ca. 5 cm; vegetation was removed by pitchfork; the plot cleared by manual raking; and 1.3 kg of 17-5-10 complete fertilizer applied.

During the nights of 6-13 September and 14-15 September 1983, the 18 plots were each inspected 5 times per night for the presence of adult M. latipes. Nightly plot inspections commenced at 18:00 hrs, 21:00 hrs, 01:00 hrs, 04:00 hrs, and 07:00 hrs. The plot-to-plot sequence for the observations initiated at each of these times was kept fixed for all times and nights; regarding field layout, the visitation sequence was conducted systematically.

Each plot was examined by entering a 4 m side and slowly moving through the vegetation in an ill-defined,

zig-zag path that roughly approximated the plot's long axis. At every second or third step, movement through the plot was paused and the vegetation carefully scanned for M. latipes adults. A clear-lensed, 6-volt, headlamp fitted with a duct tape visor aided observation. A multiple-key laboratory counter was used to simultaneously record the number of moths resting on foliage, the number of moths ovipositing, and the number of in copulo moth pairs. Moths observed flying over the plot were not counted.

Data were analyzed for differences in moth abundance in the different aged plots, differences in the number of moths present in the field per night, and differences in observed moth behavior during the various times of night. Tests for significance and confidence interval constructions were at the ($\alpha = 0.05$) level.

Vertical Movement of Larvae

During the nights of 21-30 October 1983, the movements of M. latipes larvae on potted plantings of Callie giant bermudagrass cultured under field conditions were studied. Five days prior to data collection, freshly-dug clumps of 25-day-old grass were transplanted to 20 cm diameter plastic pots filled with a 1:1:1 mixture of peat, Arredondo fine sand, and vermiculite. Thirty such pots were prepared. Each pot was placed in a 20 cm diameter plastic potting saucer. The saucers were filled with tap water at 48 hour intervals, and each received ca. 300 ml of plant nutrient solution 96 hrs post-transplant. Each pot was fitted with a

Figure 1. Field arrangement of the caged pots containing Callie giant bermudagrass, C. dactylon, used to monitor the vertical movements of M. latipes larvae. Screen enclosures are positioned to provide 44 cm of vertical free space for larval movement.

20 cm x 48 cm cylindrical cage; these were constructed by bending a 48 cm x 70 cm rectangle of 16-mesh aluminum screen into a crude cylinder and stapling the 70 cm edges. A spring-steel paper clamp fastened the base of a cage to the rim of a pot. The top of each cage was fitted with a 20 cm diameter plastic potting saucer held in place by plastic clothespins. All cages were adjusted on their pots to give a uniform distance of 44 cm from the soil surface to the inner surface of the cage top. The caged pots were arranged in a single row along a roto-tilled alleyway adjacent to a University of Florida Campus Agronomy Farm field planted to Callie giant bermudagrass (Figure 1).

During the night of 20 October 1983, a single, field-collected, 5th or 6th instar M. latipes larva was placed on the foliage in each pot. Beginning on 21 October, the position of these larvae was determined by the following procedure: a caged pot was carefully lifted from its site in the alleyway and placed on a nearby table, the vegetation examined until the larva was found, the distance from the surface of the potting soil to the headcapsule of the larva was measured (to the nearest centimeter) by reading an upheld meterstick positioned along the screen, the pot was returned to its field site, and the process repeated until all 30 pots had been examined.

Every pot was examined 8 times each night; measurements of larval position in each pot were initiated at 17:00 hrs, 18:00 hrs, 21:00 hrs, 23:00 hrs, 03:00 hrs, 06:00 hrs, 07:00

hrs and 08:00 hrs. Pot examination sequence was systematic (i.e., fixed order, based on field position).

In a few instances, a final instar larva pupated while in a pot; these were replaced. Larval replacement was done in a manner that minimized its impact on data integrity. On 25 October the larva in each pot was replaced with either a 3rd or 4th instar larva, and during 26-30 October the same procedures and measurements that were applied to the 5th and 6th instar larvae (as described above) were used to record the behavior of the 3rd and 4th instar larvae.

Hourly measurements of temperature, rainfall, and relative humidity during the experimental interval were obtained from the Agronomy Farm's weather data facility.

Data were evaluated for differences in larval position per time of night, and for differences between larvae of the two different age groups. All tests for significance and confidence interval constructions were at the ($\alpha = 0.05$) level.

Evaluation of a Grassland Sampling Device

A two-wheeled, manual, pushcart sampler capable of a 50 cm swath was constructed by suspending an open-fronted, aluminum-framed, screen cage from a crossmember-type, steel chassis (Figure 2). A complementing series of 3 slots, spaced at 5 cm intervals, were milled into the leading margin of each wheel stanchion; when fitted with the axle of a 68.6 cm diameter bicycle wheel, these slots permitted adjustment of the cage floor to heights of 5, 10 or 15 cm

above the soil surface (Figure 3). The forward edge of the cage floor was fitted with a removable, multiple-tined, forward-projecting rake head; tine spacing could be adjusted by either removing or installing individual tines at 5 cm intervals along the head's length (Figure 3).

The device was taken to the University of Florida's Campus Agronomy Farm and a series of tests was conducted to evaluate machine performance, sturdiness, and the sampling methodology that might best suit to sample M. latipes larvae in Callie giant bermudagrass, C. dactylon.

These tests entailed pushing the device through 25 m of a given grass, noting general machine response, and then inspecting the contents of the cage. Notes were made on the outcome of trials for all 3 of the cage's height settings, both the presence and absence of the rake head, and both 5 cm and 10 cm tine spacings. Larvae captured by the device were watched in situ, and notes were made on their initial location, response to the cage, and tendency to escape.

The efficacy of this device as an absolute density estimator of M. latipes larvae in Callie giant bermudagrass was evaluated by a mark-release-recapture study. Ten day old M. latipes larvae that had been greenhouse-reared on Callie giant bermudagrass were marked with fluorescent powder and released in 5 field plots of 24 day old Callie giant bermudagrass. Each plot was 0.5 m wide and 2.0 m long. At 22:00 hrs on the nights of 8 October through 11 October 1984, 30 marked larvae were released per plot. On

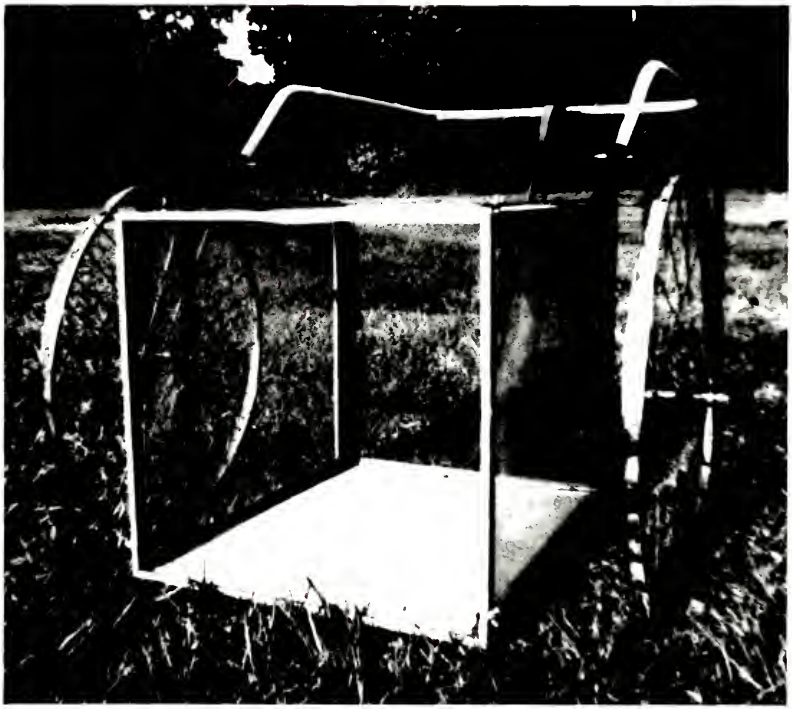

Figure 2. A pushcart device for sampling M. latipes larvae in forage grasses.

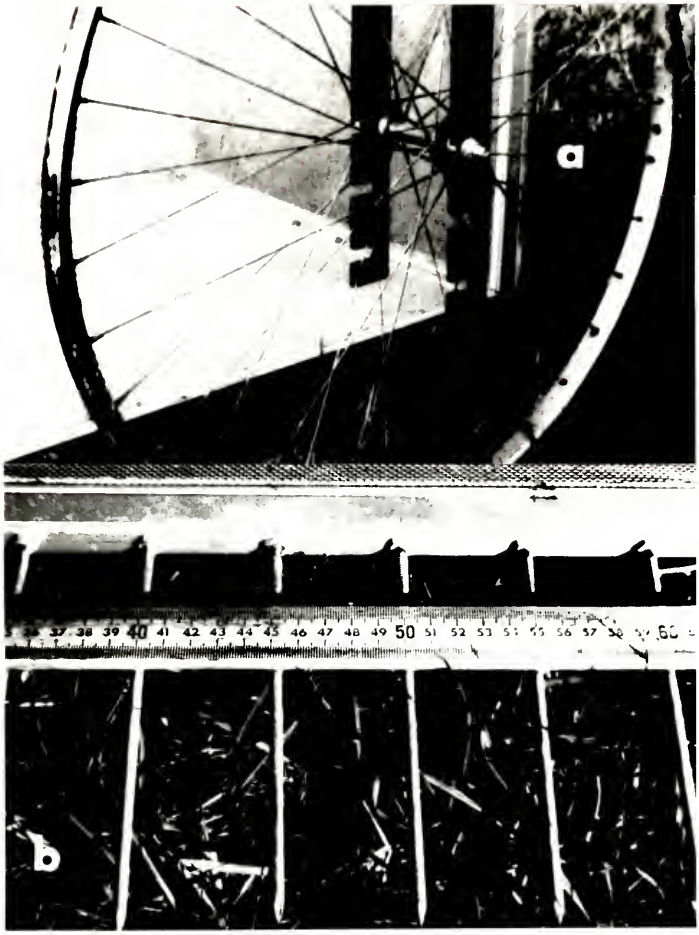

Figure 3. Adjustable features of the pushcart sampler.
a) Wheel stanchion with slots milled at 5 cm intervals; when set as shown, sampler's ground clearance is 5 cm.
b) Removeable rake head with tine spacing set at 5 cm; individual tines are threaded to permit spacing adjustments.

each of the 4 release nights, the larvae were marked with a different color (either Day-Glo® pigment no. 15, 16, 18, or 21) and left to move freely through the foliage until the following 07:00 hrs, whereupon each plot was sampled by making a single pass with the sampling device and subsequently counting the number of marked larvae found in the cage. Marked larvae were detected with the aid of a hand held, 12 volt, 366 nm longwave ultraviolet lamp. After having been counted, the larvae were removed from the cage and returned to the plot from which they had been captured. The plots were left undisturbed until the following 20:00 hrs. at which time the sampling process was repeated. To account for the influences of larval mortality, emigration, or loss of markings due to molting; at ca. 30 minutes prior to both the 07:00 hr and the 20:00 hr sampling sessions, all of the plots were examined with the ultraviolet lamp and the number of marked larvae seen in each plot was recorded. All samples were taken with the chassis set for a cage-floor-to-ground clearance of 5 cm and with the foliage rake removed.

Data were analyzed for differences in the number of larvae captured per plot, for differences in the number of larvae captured per trial, and for differences in the number of larvae captured at each time of night. All tests for significance and confidence interval constructions were at the ($\alpha = 0.05$) level.

Laboratory Experiments

Chorion Consumption

Between 20:00 hrs and 08:00 hrs on the night of 12 October 1984, a single field-collected moth deposited 86 ova on the wall of a ca. 400 ml plastic cup and then died. The dead moth was removed and the ova were incubated *in situ* at 23° ± 1° C. Eclosion commenced at 21:00 hrs on 16 October and continued until 03:00 hrs on 17 October, by which time a total of 82 larvae had emerged (the remaining 4 ova never hatched). Newly emerged larvae were removed only after they had crawled to the cup's lid (upon which no ova had been deposited) or were seen dangling from a silken thread that they had spun from the lid. After all larvae had been removed, the cup was carefully cut into several sections and each was viewed with a microscope.

The post-eclosion chorion remains of 10 randomly selected *M. latipes* ova were examined at 45X magnification with a binocular dissecting microscope. This was replicated 8 times. Each ovum in every replicate was examined twice and on both occasions was accorded a scalar value that corresponded to the proportion of the chorion that had been consumed by an emerging larva. These values ranged from 1 to 5; where, a value of 1 indicated that the spheroidal portion of a post-eclosion chorion was intact except for a circular emergence hole that constituted no more than one-sixth of the sphere's surface; the values 2, 3, and 4 indicated that the emerging larva had consumed at least one-

third, one-half, or two-thirds of the spheroidal portion, respectively; and the value 5 was assigned in those cases where essentially all of the chorion excepting the flattened base (cemented to the ovipositional surface) had been eaten by the emerging larva.

Data were analyzed for differences in the average amount of chorion consumed per replicate and for differences in the relative proportions of the various consumption categories. All tests for significance were conducted at the ($\alpha = 0.05$) level.

Early-Instar Feeding Surface Preference

Primary stems of Callie giant bermudagrass, Cynodon dactylon, were collected from the field, sealed in plastic bags, and transported to the laboratory. To avoid excessive wilting, all plant material was collected at 22:00 hrs. In the laboratory, a stem with undamaged terminal growth was cut in the vicinity of its penultimate node and the basal portion discarded. The terminal portion was placed in a 25 cm x 150 cm plastic petri dish that had been fitted with a size 14, Hercules® C-5, clarifying filter. When the plant material was placed in the petri dish, the filter disc was saturated with ca. 10 ml of tap water. Particular care was taken to position the grass foliage on the filter disc such that both the upper and lower surfaces of the blades were not in contact with either the filter disc or the petri dish cover and blade contact with the petri dish wall was minimized. A total of 6 such dishes were set up.

With the aid of an artist's brush, 10 first instar M. latipes larvae (ca. 3 hrs old) were placed on each filter disc. The petri dishes were covered and the larvae observed until they moved onto the foliage. All dishes were kept at 23° ± 1° C with a 13L:11D photoperiod.

The larvae in each dish were viewed at ca. 12 hour intervals; and when these began to exhibit signs of having entered the first pre-molt stage, the number of hours elapsed since petri dish introduction was recorded and the larvae were tranferred en masse to a second petri dish that had been prepared as described above. The plant material upon which they had fed as first instars was retained for microscope examination.

The upper and lower surface of each grass blade was inspected at 15X magnification with a binocular, dissecting microscope and the number of feeding scars found on each surface was recorded. Records were kept dish-specific. In due process, the entire procedure was repeated for the 6 petri dishes of resultant second instar larvae.

Data were analyzed for differences in the number of feeding scars on upper versus lower surfaces of blades, for differences in the average number of feeding abrasions per petri dish, and differences in the number of feeding abrasions produced by first instar larvae versus second instar larvae. All tests for significance were conducted at the ($\alpha = 0.05$) level.

Stage-Specific Developmental Time

Thirty-eight M. latipes ova that had been deposited between 20:00 hrs and 08:00 hrs on the night of 29 September 1984 by a field-captured moth were incubated in situ at 23° ± 2° C and monitored for their developmental progress. Eclosion was observed and the time recorded.

The 38 larvae were reared in isolation. Each larva was placed in a 25 cm x 150 cm plastic petri dish that had been fitted with a tap-water saturated, size 14, Hercules® C-5, clarifying filter disc. Every larva was supplied ad libitum quantities of freshly-cut Callie giant bermudagrass, Cynodon dacytlon, foliage. Frass and plant debris were removed from petri dishes as needed. Rearing conditions were kept fixed at 23° ± 2° C with a 13L:11D photoperiod until all larvae had pupated.

All dishes were inspected at ca. 12 hour intervals (at noon and midnight ± 3-4 hrs) and the developmental progress of each larva was noted and recorded.

Pupal development was monitored in a similiar fashion. Pupae were left undisturbed until cuticular pruinescence was observed; whereupon, they were removed from their cocoons, sexed, and weighed. Each pupa was placed in a 30 ml plastic cup and held for adult emergence.

Adults were killed and spread for voucher specimens; these were placed in the arthropod collection housed by the Florida Division of Plant Industry in Gainesville.

Data were analyzed for determination of the mean developmental time for each stage of the life cycle and mean pupal masses; the latter were determined gender-specifically. All significance testing was conducted at the ($\alpha = 0.05$) level.

RESULTS AND DISCUSSION

Field Experiments

Moth Attraction to Different Host Grasses

Rain fell only once (1.1 mm during 18:50 - 19:45 hrs on 21 September); mean hourly temperature and relative humidity were 20.2° ± 0.6° C and 86% ± 2%, respectively.

In 320 observations of the control receptacles, no adult M. latipes were seen resting on the poultry wire. These data were excluded from the remaining analyses.

A chi-square test of the total counts for moth visitation, on a per grass basis, indicated that the visitation ratio was significantly ($\chi^2 = 274.88$; df = 2) different than that hypothesized (H_o: ratio of visitation to the three grasses is 1:1:1). When the same type of test was applied to overall counts of moth abundance across nights, the resultant test statistic proved too low ($\chi^2 = 1.33$; df = 3) to reject a hypothesized homogeneity of nightly visitations. Thus the incidence of moth visitation was significantly different for each of the three grass species, but was more or less uniform from night to night.

It seems likely the short study period, stable weather conditions, and single test site reduced experimental variability and increased the across-night homogeneity of moth

behavior. Undoubtedly, test-grass condition and moth population intensity were key elements as well. Quantitatively, both were unknowns; however, assignment of ten culms per sample unit probably compensated for variations in the former, and the latter was of damaging (i.e., sufficient to merit an application of methomyl to the surrounding research fields on 26 September) proportions.

In 960 viewings of the receptacles containing the three grasses, 197 adult M. latipes were seen resting on 153 different sample units. Of these, 175 moths on P. notatum racemes (135 sample units); 4 moths on D. sanguinalis racemes (4 sample units); and, 18 moths rested on C. dactylon culms (14 sample units). Thus, in an overall context, the number of moths per sample unit was sharply skewed (i.e., evinced a comparatively high frequency of zero counts).

Evaluation of test statistic U and its accompanying standard error [SE(U)], as applicable to count data evincing high frequencies in the zero class (Elliott 1977), revealed the negative binomial frequency distribution could not be rejected ($\hat{a} = 0.3849$; $U = -0.01038$; $SE(U) = 0.01079$) as a defining function for these data. Parameter estimation (by iterative solution when applicable) subsequently yielded: $\bar{y} = 0.2053$, $s^2 = 0.2738$, and $k = 0.5511$, for the distribution's mean, sample variance, and descriptive constant, respectively. Three points merit mention. First, since the interval delimited by the absolute value of SE(U)

contains the value obtained for U, fit of the indicated distribution function is accepted at an error level slightly less than $\alpha = 0.05$. Second, the value obtained for the constant (k) lies between zero and one; an indication that contagion characterizes the count data (hence, the Poisson function would be a poor choice). Third, the value obtained for the distribution's mean ($\bar{y}$) suggests the "overall success rate" for observing a moth visiting a sample unit was "fairly good" (i.e., one-fifth moths per sample unit) notwithstanding the dilution that resulted from including the comparatively "unattractive" D. sanguinalis sample units. The principal utility of such a finding is simple: the data warrant further, and parametrical, analysis.

Application of Taylor's Power Law to these data, via the methodology set forth by Elliott (1977), revealed the mean's dependence upon the variance was adequately described by: $\sigma^2 = 2026.0493\mu^{5.5934}$. Subsequent employment of this expression, coupled with consistent integer elevation of all original data points, yielded: $y \rightarrow (y + 1)^{-1.79672}$ as a transformational expression capable of rendering the mean independent of the variance, thus establishing a valid basis for applying parametrical statistical procedures.

An analysis of variance revealed that three factors (grass species, time of night, and grass x time interaction) contributed significantly to the overall experimental variability Moreover, both the effect due to whole unit blocks and the subunit block-time interaction were insignificant

Table 1. ANOVA of transformed[a] counts of adult *M. latipes* visitation to culms of *P. notatum*, *C. dactylon*, and *D. sanguinalis* at eight different times of night.

Source	SS	df	MS	F_{calc}
Blocks	2.49035	39	0.06394	0.8338
Grasses	18.72331	2	9.36166	122.0715*
$Error_a$	5.98168	78	0.07669	
Whole Unit	27.19534	119		
Times	4.34238	7	0.62034	14.5757*
Grass x Time	5.33850	14	0.38132	8.9596*
Block x Time	12.86814	273	0.04713	1.1075
$Error_b$	23.23805	546	0.04256	
Total	72.98241	959		

[a] Counts transformed by: $y \rightarrow (y + 1)^{-1.79672}$.

* Values followed by asterisk (*) significant at the $\alpha = 0.05$ level.

(Table 1). In combination, an insignificant F-statistic for both the whole unit blocks and the subunit block-time interaction indicates that the overall field positioning of the receptacles had a negligible influence on the observed variability in moth visitation. More particularly, an insignificant effect for whole unit blocks is an indication that the moths displayed no inclination to rest on the sample units in one block over those in another; whereas, insignificance of the subunit block-time interaction indicates that the number of moth visitations recorded within a block at a specific time did not significantly affect the number of moth visitations recorded for the same block at either the preceding or following times. This is a critical point, for if otherwise had been the case, the effect that time of night has on moth visitation to the three grasses could not have been evaluated via these data.

Comparison of the mean number of moth visitations per grass indicate that more moths chose to rest on racemes of P. notatum, and that moth visitations to D. sanguinalis and C. dactylon culms were statistically equivalent (Table 2). These data highlight two notable issues. First, (recalling no moths landed on the poultry wire controls) it seems clear that M. latipes adults select their resting sites discriminately. Second, it seems unlikely that these moths cued mainly on plant profile, for, a ten culm cluster of P. notatum physically resembles a comparable-sized cluster of D. sanguinalis culms, yet, the evidence indicates the moths

Table 2. Overall mean abundance[a] of adult M. latipes per 10-culm cluster of P. notatum, D. sanguinalis, or C. dactylon assayed under field conditions.

Grass Species	Mean[b,c]		95% Confidence[d] Interval
P. notatum	(0.236)	0.684	0.726 , 0.641
C. dactylon	(0.019)	0.967	1.010 , 0.924
D. sanguinalis	(0.005)	0.991	1.034 , 0.948

[a] Means are each of n=320 observations, with these the result of moth counts taken hourly from 19:00 until 03:00 on four different nights.

[b] Values enclosed by parentheses are detransformed point estimates.

[c] Determined from count data transformed as follows:

$$y \rightarrow (y + 1)^{-1.79672}.$$

[d] Confidence intervals are constructed about transformed means.

overwhelmingly opted to visit and rest on culms of the former rather than those of the latter.

At present, P. notatum is the dominant vegetation of at least 2.5 million acres of Florida pasture (Johnson et al. 1975), and covers an undocumented (but large) amount of road right-of-way, airport grounds, playing fields, parks, schoolyards, and lawns. In their investigations of adult velvetbean caterpillar (VBC), Anticarsia gemmatalis Hubner, Greene et al. (1973) reported finding VBC adults resting on P. notatum racemes. When these two facts are coupled with the evidence presented above, a scenario with potentially profound implications emerges: the acreage sustaining this grass may well be a reservoir of a substantially attractive plant species that is tapped by two economically injurious noctuids. Thus, the presence of P. notatum throughout the state may be facilitating the migratory behaviors of agriculturally important moth species.

M. latipes' response to the sample units was influenced by time (Table 1). Hartstack et al. (1979) have noted that sampling and monitoring conducted during peak moth activity periods may be the superior way to forecast both larval populations and crop damage. Such efforts presuppose time-specific knowledge of moth behavior. Time-specific differtials in adult M. latipes abundance per sample unit on each of the three grasses are presented in Table 3.

Moths were simultaneously present on all three grasses only during 20:00 hrs (Table 3). In light of the extremely

Table 3. Time-specific abundance of a field population of adult *M. latipes* on 10-culm clusters of either *P. notatum*, *C. dactylon*, or *D. sanginalis*.

	P. notatum		*C. dactylon*		*D. sanguinalis*	
Hour	Mean	Std.Err.	Mean	Std.Err.	Mean	Std.Err.
19:00	0.827	0.032	0.982	0.032	1.000	0.032
20:00	0.531	0.045	0.904	0.045	0.947	0.045
21:00	0.470	0.035	0.978	0.035	1.000	0.035
22:00	0.543	0.042	0.907	0.042	1.000	0.042
23:00	0.530	0.037	0.964	0.037	1.000	0.037
24:00	0.765	0.033	1.000	0.033	0.982	0.033
01:00	0.907	0.023	1.000	0.023	1.000	0.023
02:00	0.889	0.024	1.000	0.024	1.000	0.024

Means are of n=40 observations per grass per time.

Values reported are those obtained from analysis after transformation of original moth counts.

Transformation given as: $y \rightarrow (y + 1)^{-1.79672}$.

low number of moth visitations to the D. sanguinalis culms, such a finding could either be the result of coincidence or could be indicative of some as yet poorly understood aspect of this moth's behavior. Although the evidence is insufficient for definitive judgement, the latter interpretation seems somewhat more likely since moth abundance on the two minimally visited grasses (i.e., C. dactylon and D. sanguinalis) evinced similiar trends between 19:00 hrs and 21:00 hrs, while moth abundance steadily increased on the P. notatum during the same interval (Table 3). Undoubtedly, these time-specific shifts were instrumental in rendering the subplot interaction term (Table 1) significant.

The time specificity of M. latipes' behavior is better seen when examination of the data presented in Table 3 is focused on moth abundance per time on P. notatum. At 19:00 hrs, moths were present in low numbers. Moth population intensity increased dramatically during the ensuing hour, and by 20:00 hrs, had essentially peaked. This condition remained substantially unchanged (i.e., the means were not significantly different) for the next three hours. At 24:00 hrs, moth abundance per sample unit had declined, and by 01:00 hrs fewer moths were seen resting on P. notatum culms than had been present during the 19:00 hr count. This condition (very few moths) aptly describes the remainder of the assay period. Thus, moth activity on P. notatum evinced a cyclical (unimodal and platykurtic) character nightly during the period from 19:00 hrs to 01:00 hrs (Table 3).

The dramatic increase in the number of moths seen resting per sample unit of P. notatum that occurred during the 19:00 to 20:00 hr interval has a utilitarian implication: this time frame will likely prove a poor period to undertake quantitative assessments of M. latipes populations, for it combines a relatively short time interval with an expectation of high sample variance; these two features antagonize most sampling schemes. Conversely, moth counts taken during the interval from 20:00 hrs through 23:00 hrs indicate this time frame was one in which the moth population was both comparatively high and essentially stable. The implication here is that this may prove the better time to estimate adult populations of M. latipes in fields planted to P. notatum.

None of the M. latipes adults counted during the experimental period were seen to either copulate or oviposit. Visual inspection of those sites chosen by moths who rested on sample units of either C. dactylon or D. sanguinalis yielded no tangible evidence to link the moths' presence to eitner of these two hosts. In contrast, in virtually every instance that a moth was seen resting on a sample unit of P. notatum, the moth was clinging to the grass inflorescence (raceme), had its proboscis extended, and was probing the raceme's surface and crevices. In most of the instances that this activity was observed, the region of the raceme probed by the moth glistened with smears or droplets of a clear liquid (Figure 4).

Figure 4. Male Mocis latipes (Guenée) resting on a Paspalum notatum Flugge raceme. The distal aspect of the moth's proboscis probes a clear liquid coating a localized region of the raceme. The dark blotches on the raceme are floral parts. The moth in the background is Anticarsia gemmatalis Hubner.

Karr (1976) observed noctuids congregating on roadside stands of Paspalum virgatum L. growing near Fort Clayton, Canal Zone. In describing the grass, he stated, "Four of the inflorescences had open spikelets with a sticky, almost mucous, and sweet-tasting fluid . . . ." and that, ". . . by 19:15 moths were being attracted to the inflorescences with open spikelets . . ." (Karr 1976, p. 284). Similiarly, while investigating a stand of P. virgatum growing along a canal near Cardenas, Mexico; Lloyd (1981, 1984) noted that predator fireflies and their prey fed on a sticky substance coating the grass seed heads. The descriptions put forward by these researchers closely parallel the evidence offered above, and in large part, serve to corroborate the suspicion that the behavioral link between the observed high degree of visitation by adult M. latipes to racemes of P. notatum is that the moths are utilizing a plant-derived substance as a food source.

Moth Activity in Callie Giant Bermudagrass

The magnitudes of the F-statistics obtained via an analysis of variance of the moth count data indicate that grass age and time of moth counts were the principal sources of variability in moth abundance (Table 4). Hence, there were more M. latipes adults present in plots containing grass of one age than in comparable-sized plots containing a different age of grass; moreover, more moths were seen at one time of night than another. This implies that moth behavior is modified both by host plant age and by short

Table 4. Summary of three-way, split-plot ANOVA of adult M. latipes abundance in three different ages of Callie giant bermudagrass, C. dactylon, at five different times of night.

Source	df	F_{calc}	F_{tab}
Nights[a]	7	6.84	2.09
Grass Age[b]	2	167.78	3.07
Night x Age	14	2.54	1.75
$Error_a$	120		
Time[c]	4	115.32	2.37
Night x Time	28	7.94	1.48
Age x Time	8	21.14	1.94
Night x Age x Time	56	2.44	1.33
$Error_b$	480		

[a] Defined as the scotophasic interval commencing at 18:00 hrs and ending at 07:00 hrs; moth counts were made during this interval for the period 6 September through 13 September 1983, and 14 September to 15 September 1983.

[b] Above-ground plant growth in a given plot on 6 September 1983 was either A=15, B=25, or C=35 days old.

[c] Moth counts commenced at 18:00 hrs, 21:00 hrs, 01:00 hrs, 04:00 hrs and 07:00 hrs.

term, temporal change. Such information is quite desirable; for, when elucidated with specifics regarding grass age and time of night, it provides a framework for an adult moth monitoring program that is based upon characteristics of the moths' behavior.

Further examination of these data (Table 4) shows that a straightforward specification of the differences in moth abundance due to effects of either grass age or the time of night (partitioned per age or per time) is not forthcoming via paired comparisons between levels within factors, for factors other than these two also made significant contributions to experimental variability. Moreover, in all cases but one (the effect of nights), these are interaction terms; hence, the relationships between main effects (i.e., nights, grass age, and time) are such that experiment-wide comparisons utilizing a common variance prove nonorthogonal. Thus the value of the ANOVA is twofold: all three of the main effects merit further scrutiny, and the analysis of each will be better rendered through partition.

During the period for which moth activity in Callie giant bermudagrass was measured, a total of 2270 individual moth sightings were recorded. With respect to nights, this number yields 283.75 ± 64.78 as the 95% confidence interval (df = 7) about the expected value for moth abundance per night. Only one night's moth count (the data obtained for the night of 14-15 September, 1983) is not contained by this interval (Fig. 5). Undoubtedly, retention of this night's

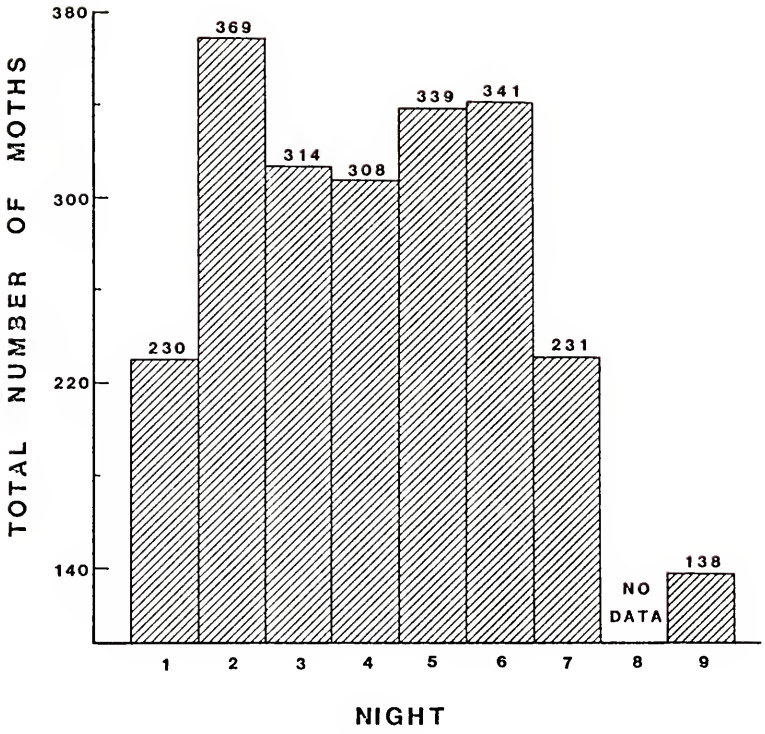

Figure 5. Histogram of adult M. latipes abundance[a] per night during 6 September to 15 September 1983 in a field of Callie giant bermudagrass.

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[a] Determined by counting the number of moths seen on the foliage in 18 different 4 m x 12 m plots of grass; moth counts in each plot were repeated at 5 different times (18:00, 21:00, 01:00, 04:00, and 07:00 hrs) each night.

moth count in the overall data set substantially affected the effect due to nights. Conversely, its exclusion (which would make counts per night more homogeneous) would reduce the number of degrees of freedom available for subsequent analysis.

Total moth abundance per night was at one of three levels; moreover, these were juxtaposed in a decidedly non-random configuration (Fig. 5). At the onset of data collection the nightly count was 230 moths (level 2), followed by a sharp increase that remained essentially stable for the five ensuing nights (level 3), and thereafter declined (at a rate virtually identical to that of the original increase) to a low of 138 moths (level 1) for the ninth night. Thus the heterogeneity detected by the ANOVA was of an orderly sort (i.e., more or less normally distributed about a sustained peak), and is perhaps best explained as being a natural consequence of emigration, immigration, natality (in the sense of moths being "born" from mature pupae), and mortality forces in a field population of M. latipes adults.

Every night, significantly more moths were present in the plots containing the oldest grass than in those having either of the other two grass ages (Fig. 6); however, moth presence in the intermediate age grass compared more favorably with that noted for the oldest grass than it did for the moth presence detected in the youngest grass (moth presence in this last was near-inconsequential). These

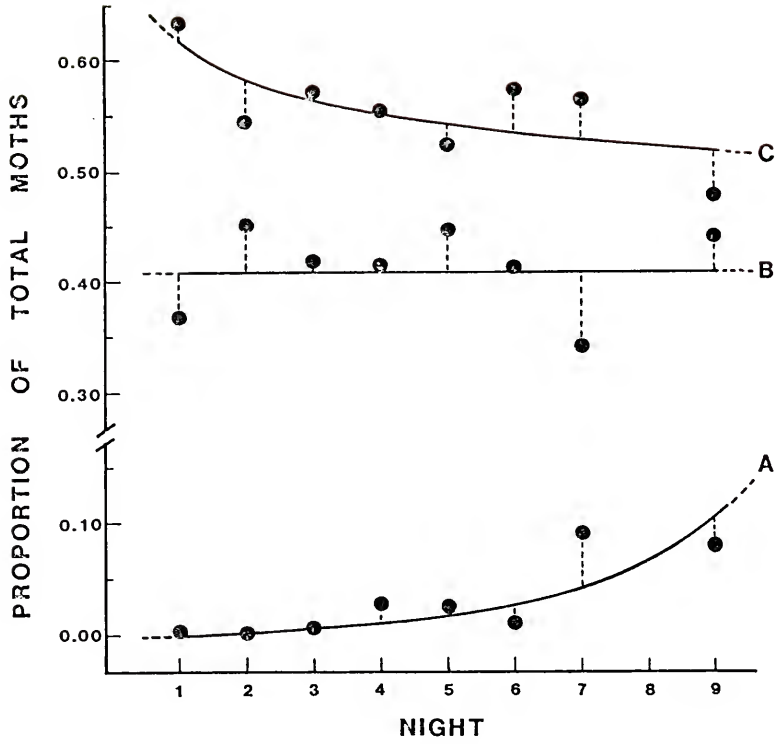

Figure 6. Least-squares regression functions describing changes in adult M. latipes abundance in plots containing different ages of Callie giant bermudagrass, C. dactylon, during the period from 6 September to 15 September, 1983. Functions A, B, and C correspond to moth populations in grass plots aged 15 to 24, 26 to 35, and 35 to 44 days, respectively.

differences are the reason that the F-statistic for the effect due to grass age (Table 4) proved significant. However, neither the moth population per night nor the proportion of moths present per grass age remained static for the experimental period; a fact indicated by the significant value of the night x age F-statistic (Table 4). The data presented in Figure 6 illustrate this phenomenon.

In those plots containing the oldest grass (age C), the proportion of the total moths present each night declined in a curvilinear ($Y = 0.6161 - 0.0443 \text{ Log}_e X$) manner; but the proportional presence of moths in the youngest grass (age A) evinced a curvilinear ($Y = 0.0023 + e^{0.4302 X}$) increase through time. Moth presence in the intermediate aged grass (age B) remained essentially unchanged ($Y = 0.4078 + X$) from night to night (Fig. 6).

The mechanism underlying the observed differences in moth presence in the different ages of grass is a consequence of related biological phenomena acting in concert. Several points support this position. First, since all of the plots were in the same field and in close proximity (neighboring plots were separated by a 75 cm alleyway), differences in moth presence due to differential accessiblity of plots seem unlikely. Second, the plant growth in plots of different ages was substantially different. The plots containing the youngest grass (age A) had very few primary stems higner than ca. 25 cm, and in consequence, lacked a closed plant canopy (i.e., the soil surface was readily

visible). In contrast, plots containing either the intermediate or the oldest grass (ages B and C, respectively) had primary growth at least 45 cm high and well-closed canopies (i.e., less than 5% of the soil surface readily visible). Third, to successfully produce progeny, an adult moth must display some measure of gregariousness. In result, the presence of one moth in a given plot enhances the likelihood of observing a second nearby. Concatenation of these points yields a scenario that helps to explain the observed differential in moth presence set forth in Figure 6.

By having more above-ground plant growth, the plots with the two older grass stands provided the moths with a greater diversity of resting sites, ovipositional sites and sheltered areas; and, moths that entered these plots in response to these physical conditions rendered them more attractive to sibling moths, particularly those seeking mates.

Within nights, moth abundance per time was decidedly non-uniform. Regardless of grass plot age, more moths were present at 21:00 hrs; this was the only time of night that moth presence in the youngest grass was statistically different from zero (Table 5). The time of night determined as the period of peak abundance also proved to be both the only time of night that M. latipes adults were observed ovipositing (Table 6) and the earliest time of night that in copulo pairs were observed in plots containing the two older grass ages (Table 7).

Table 5. Summary statistics of adult M. latipes abundance[a] in three different ages of Callie giant bermudagrass, C. dactylon, at five different times of night.

	Grass Age[b]					
	A		B		C	
Time	Mean	Std.Err.	Mean	Std.Err.	Mean	Std.Err.
18:00	0.13	0.087	3.75	0.539	4.69	0.488
21:00	0.83	0.172	7.63	0.643	9.19	0.543
01:00	0.10	0.104	4.38	0.459	6.40	0.557
04:00	0.10	0.104	2.29	0.328	4.00	0.453
07:00	0.04	0.042	1.60	0.226	2.17	0.363

[a] Determined by counting the number of moths seen on the foliage in 4 m x 12 m plots of grass.

[b] Grass ages A, B, and C correspond to above-ground grass plant regrowth aged 15 to 24, 26 to 35, and 35 to 44 days, respectively.

Means and their accompanying standard errors are each of n=48 observations.

Table 6. Summary statistics of the proportions[a] of an adult M. latipes population observed ovipositing in Callie giant bermudagrass, C. dactylon, plots of two different ages at five different times of night.

Grass Age B (26 to 35 days of regrowth)				
Time	Mean	Std. Err.	Precision[b]	n
18:00	0.00	0.000	---	48
21:00	0.23	0.024	10.43	48
01:00	0.00	0.000	---	48
04:00	0.00	0.000	---	48
07:00	0.00	0.000	---	48
Grass Age C (35 to 44 days of regrowth)				
Time	Mean	Std. Err.	Precision[b]	n
18:00	0.00	0.000	---	48
21:00	0.21	0.018	8.57	48
01:00	0.00	0.000	---	48
04:00	0.00	0.000	---	48
07:00	0.00	0.000	---	48

[a] The number of ovipositing moths seen in each of forty-eight plots divided by the total number of moths seen per plot. Each plot measured 4 m x 12 m.

[b] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

Table 7. Summary statistics of the proportions[a] of an adult *M. latipes* population observed *in copula* in Callie giant bermudagrass, *C. dactylon*, plots of two different ages at five different times of night.

Time	Mean	Std. Err.	Precision[b]	n
Grass Age B (26 to 35 days of regrowth)				
18:00	0.00	0.000	---	48
21:00	0.07	0.017	24.29	48
01:00	0.31	0.041	13.23	48
04:00	0.20	0.052	26.00	48
07:00	0.00	0.000	---	48
Grass Age C (35 to 44 days of regrowth)				
18:00	0.00	0.000	---	48
21:00	0.19	0.030	15.79	48
01:00	0.23	0.047	20.43	48
04:00	0.16	0.039	24.38	48
07:00	0.00	0.000	---	48

[a] The number of *in copula* moths seen in each of forty-eight plots divided by the total number of moths seen per plot. Each plot measured 4 m x 12 m.

[b] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

Viewed overall, the time specificity evident in these data (moth abundance per time of night, ovipositional activity, and incidence of mating) strengthens the interpretation put forward earlier: manifest differences in moth abundance in plots of different ages is substantially influenced by factors that are consequences of moth presence per se. When the data for ovipositional activity are considered separately, the role of the host comes into sharper focus: moths oviposited only in the plots containing either of the two older grasses; moreover, the proportion of moths per plot doing so were statistically identical for the two grass ages (Table 6). Apparently, when given the choice between ovipositing on relatively new growth (that lacks a closed canopy) and older growth (that affords more cover), M. latipes females will overwhelmingly opt for the latter. Although it will likely be a rare event that a bermudagrass field in a production situation will have more than one age of grass in it at any given time, the information put forward here is valuable in two regards. First, untended grass stands adjacent to production areas that lack closed canopy may well possess attributes conducive to moth population buildup (e.g., be old enough to have closed canopy), with subsequent encroachment of the production site a likely short-term option. Second, field scouting/sampling activities conducted in fields whose above ground plant growth is less than 3 weeks old will likely be of marginal value.

Figure 7. M. latipes mating in Callie giant bermudagrass, C. dactylon. Orientation is female superior.

In contrast to the pointedly time specific character of ovipositional activity, M. latipes adults were observed in copulo over a period of several hours each night (Table 7). Unlike ovipositional activity (where the female is in near-continuous motion, flying and hovering in the interstices of the middle and lower portions of the plant canopy, pausing only momentarily to deposit an egg (most often individually, but occasionally two) on a grass stem, sheath, ligule, or blade), copulation is a sessile act usually accomplished in the upper one-third of the grass canopy (Figure 7). In result, mating moths are easily detected by visual inspection. This raises two points that may ultimately prove of value in a monitoring program. First, sessile character and high visibility are desirable attributes if moth monitoring is to be accomplished by visual inspection; assuming this method is chosen, counting only the number of in copulo pairs per unit area may yield population estimates that are less variable than those obtained when all moths per unit area are counted. Second, these data (Table 7) indicate that after 21:00 hrs, a substantial portion of the moth population is engaged in mating; such moths are likely to be relatively unresponsive to pheromone trapping. Hence, if pheromone baited traps are to be the basis of a monitoring program, counts taken after 21:00 hrs will probably yield data that underestimate the actual populational intensity.

Vertical Movement of Larvae

Analysis of the data obtained for fifth and sixth instar larvae revealed that both a significant effect due to nights and a significant night x time interaction were the consequences of variation induced by the inclusion of measurements taken on the night 24-25 October, and that an evaluation of the effect of time of night on larval movement could be better evaluated when based on the 480 measurements taken during the nights of 21-22 and 22-23 October (Table 8). Similiar analysis of the data obtained for the third and fourth instar larvae yielded comparable findings (Table 9). In result, further analysis for each of the two data sets was applied to those measurements obtained during the nights for which homogeneity (with respect to nights) could not be rejected (i.e., n=480 per larval age group).

Fifth and sixth instar M. latipes larvae occupied different portions of the grass canopy at different times of night (Table 10). Measurements taken at 17:00 hrs indicate that these larvae rest (oriented such that the headcapsule is directed upward) on the basal portions of primary stems. During the following hour, the larvae initiate an upward movement; and by 21:00 hrs, have moved to the canopy's middle stratum (ca. 21 cm above the soil surface) and remain in this location for the ensuing next nine hours. Measurements of larval position at 07:00 hrs revealed this time to be a period of flux; and that by 08:00 hrs, the larvae had returned to the same portion of the grass canopy that they

Table 8. Summary of two-way, split-plot ANOVA of the time-specific vertical movements of fifth and sixth instar M. latipes larvae in Callie giant bermudagrass, C. dactylon.

Source	df	F_{calc}	F_{tab}
Nights†	2	3.265	3.11
$Error_a$	87		
Times*	7	96.937	2.76
Night x Time	14	5.675	1.71
$Error_b$	609		

Source	df	F_{calc}	F_{tab}
Nights††	1	0.013	4.00
$Error_a$	58		
Times*	7	69.355	2.01
Night x Time	7	0.657	2.01
$Error_b$	406		

† Scotophase beginning 21, 23 and 24 October, 1983.

†† Scotophase beginning 21 and 23 October, 1983.

* Hours at which measurements were commenced (17:00, 18:00, 21:00, 23:00, 03:00, 06:00, 07:00, and 08:00).

Table 9. Summary of two-way, split-plot ANOVA of the time-specific vertical movements of third and fourth instar M. latipes larvae in Callie giant bermudagrass, C. dactylon.

Source	df	F_{calc}	F_{tab}
Nights†	2	0.889	3.11
$Error_a$	87		
Times*	7	241.498	2.76
Night x Time	14	1.968	1.71
$Error_b$	609		

Source	df	F_{calc}	F_{tab}
Nights††	1	0.180	4.00
$Error_a$	58		
Times*	7	134.095	2.01
Night x Time	7	1.190	2.01
$Error_b$	406		

† Scotophase beginning 26, 27 and 28 October, 1983.

†† Scotophase beginning 27 and 28 October, 1983.

* Hours at which measurements were commenced (17:00, 18:00, 21:00, 23:00, 03:00, 06:00, 07:00, and 08:00).

had occupied on the previous evening at 17:00 hrs. Thus, vertical movements of fifth and sixth instar larvae evinced substantial unimodal, curvilinear, character per scotophase (Table 10).

Regression analysis (larval height as a function of time of night) of these data revealed that a second-order polynomial, $Y = -203.921 + 0.184X - 3.714x10^{-5}X^2$, could not be rejected as an appropriate (t_{calc} for β_0, β_1, and β_2 was -5.69, 6.08, and -6.05, respectively; $F_{calc} = 18.484$, df = 2,5; $R^2 = 0.881$) deterministic model for the vertical movements of fifth and sixth instar M. latipes in Callie giant bermudagrass (Fig. 8).

Like their older counterparts, third and fourth instar M. latipes larvae occupied different portions of the grass canopy at different times of night. However, the vertical movements of these larvae, although similiar in kind (i.e., upward movement in the early hours of scotophase and downward movement in the final hours of scotophase), proved unique in three regards. First, the measurements taken during 17:00 hrs and 18:00 hrs indicate that these younger larvae remained essentially immobile during this period. Second, they inhabited the middle portion (ca. 25 cm above the soil surface) of the grass canopy during the interval from 21:00 hrs to 07:00 hrs (which is at least an hour longer than the amount of time the older larvae occupied the same portion). However, the measurements obtained for the third and fourth instar larvae at 08:00 hrs were not

Table 10. Time-specific mean height[a] above soil surface of fifth and sixth instar M. latipes larvae isolated in caged pots of Callie giant bermudagrass, C. dactylon.

Time	Mean Height	Std. Err.	Precision[b]	n
17:00	3.98	0.244	6.13	60
18:00	6.42	0.804	12.52	60
21:00	20.35	1.297	6.37	60
23:00	23.45	1.528	6.52	60
03:00	20.55	1.508	7.34	60
06:00	20.85	1.399	6.71	60
07:00	8.95	1.125	12.57	60
08:00	3.58	0.271	7.57	60

[a] Distance, in centimeters, from soil surface to larval head capsule.

[b] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

Table 11. Time-specific mean height[a] above soil surface of third and fourth instar M. latipes larvae isolated in caged pots of Callie giant bermudagrass, C. dactylon.

Time	Mean Height	Std. Err.	Precision[b]	n
17:00	2.22	0.148	6.67	60
18:00	2.47	0.169	6.84	60
21:00	24.70	1.279	5.18	60
23:00	27.05	1.328	4.91	60
03:00	26.60	1.404	5.28	60
06:00	24.87	1.520	6.11	60
07:00	19.10	1.775	9.29	60
08:00	4.43	0.509	11.49	60

[a] Distance, in centimeters, from soil surface to larval head capsule.

[b] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

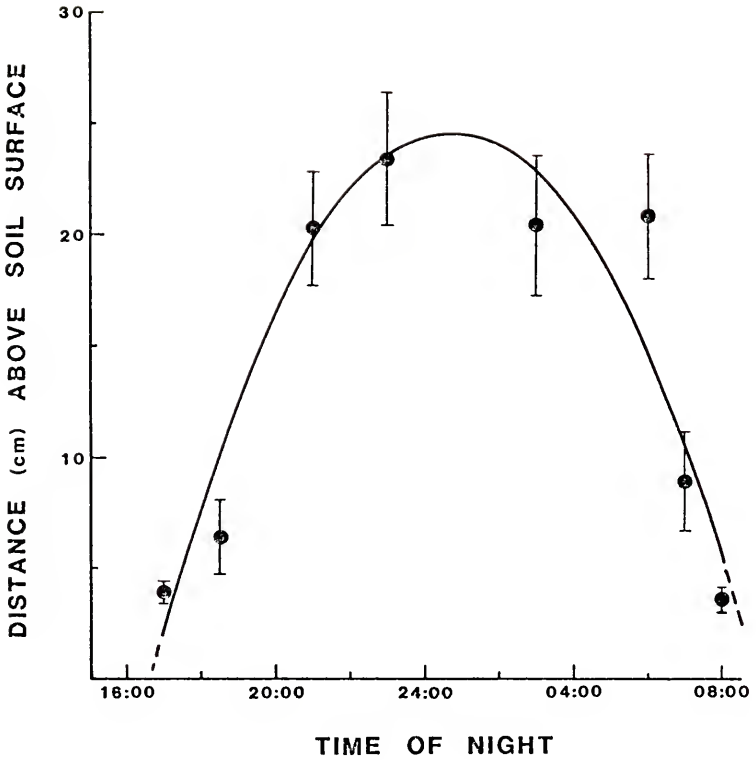

Figure 8. Deterministic polynomial model[a] describing the time-specific vertical movements of fifth and sixth instar M. latipes larvae in Callie giant bermudagrass, C. dactylon, canopy. Brackets about means indicate 95% confidence intervals.

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[a] $Y = -203.921 + 0.184X - 3.714 \times 10^{-5} X^2$.

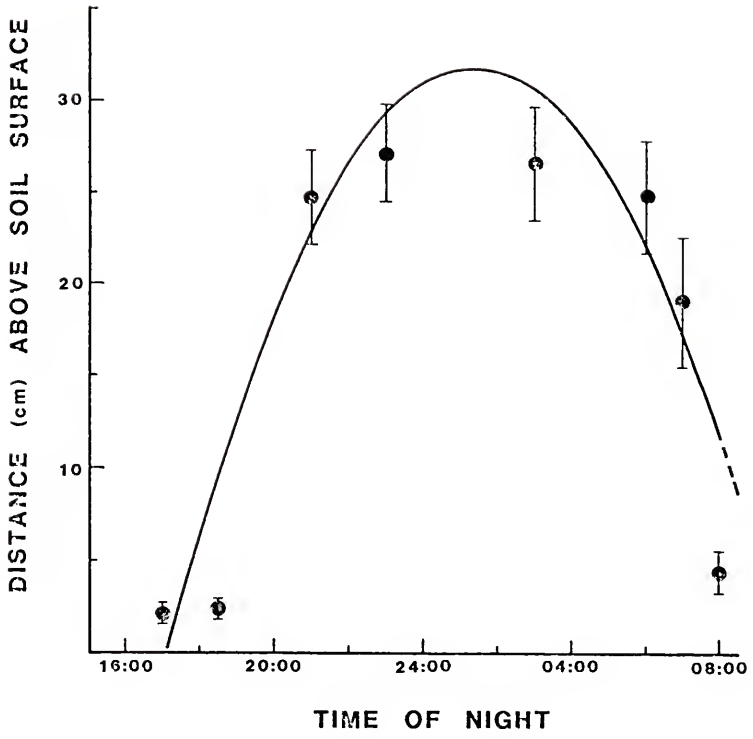

Figure 9. Deterministic polynomial model[a] describing the time-specific vertical movements of third and fourth instar M. latipes larvae in Callie giant bermudagrass, C. dactylon, canopy. Brackets about means indicate 95% confidence intervals.

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[a] $Y = -266.591 + 0.235X - 4.642 \times 10^{-5} X^2$.

statistically different from those that described the location of the older larvae for the same period. This points up the third unique feature of the data obtained for the younger larvae: these larvae required less than an hour to move from the center of the canopy to its basal portion (Table 11).

Regression analysis (larval height as a function of time of night) of these data revealed that a second-order polynomial, $Y = -266.591 + 0.235X - 4.642 \times 10^{-5} X^2$, could not be rejected as an appropriate (t_{calc} for β_0, β_1, and β_2 was -5.31, 5.53, and -5.40, respectively; $F_{calc} = 16.477$, df = 2,5; $R^2 = 0.868$) deterministic model for the vertical movements of third and fourth instar M. latipes in Callie giant bermudagrass (Fig. 9).

The overall structure of both models is quite similiar (e.g., both are curvilinear, both are second-order,and both have peaks that roughly correspond to 01:00 hrs); however, not only do they differ, but the differences they evince suggest biological interpretations that may both help to further understanding of causal relationships existing in grassland agroecosystems and aid the implementation of a sampling program that focuses on third or fourth instar larvae.

A comparative inspection of these data (Figures 8 and 9) reveals that the rate at which larvae both ascend and descend is unique for each of the two larval age groups; this is the principal difference between the two models.

The movement of fifth and sixth instar larvae from the basal portion of the canopy to its central region was initiated at least an hour earlier than comparable movements by the third and fourth instars, yet both groups were first detected in the central canopy at the same time. The decreased slope evidenced in the model for fifth and sixth instar movements reflects this difference. Similarly, the fifth and sixth instar larvae initiated a return to the lower portion of the canopy about an hour earlier than did their younger counterparts; in result, the slope of the descending phase was lessened. Although these phenomena occurred during times of change in light intensity (the times for civil sunset and sunrise during the experimental period were 19:35 hrs and 06:50 hrs, respectively), it seems unlikely that larvae of one age group are better equipped to detect these changes; hence, though a correlation is evidenced, causation is rejected in lieu of two more biologically-oriented factors: larval appetite, and predator avoidance.

Fifth and sixth instar M. latipes larvae consume significantly more grass foliage than do third and fourth instars (Reinert 1975). Since the larvae remain in the lower portion of the grass canopy (where green foliage is comparatively scarce) during photophase (Fig. 10), the daylight interval is a period of larval fasting. Hence, it is possible that the comparative reduction in the slope of the ascending phase evidenced in the model of the older larval group's movements is a consequence of these larvae responding to

hunger, and that this reaches a level sufficient to evoke movement toward green foliage at a time earlier than that evidenced for younger larvae. Since foodstuff conversion efficiency is greater in younger larvae (Reinert 1975), it does not seem unreasonable to suspect that the older larvae are prompted more readily by appetite.

Differences evidenced in the rates at which larvae of the two groups return to the lower portion of the canopy may have been due to age-specific responses of larvae to predator pressure. During September and October 1983, a large (ca. 500) flock of boat-tailed grackles, Quiscaulus major (Vieillot.), visited the experimental site every morning at dawn and were often seen searching and feeding in the grass fields. Inspection of those areas from which the birds had recently departed invariably revealed that the population of M. latipes larvae had been substantially reduced by the birds' presence.

Linkage of this predator-prey relationship to larval behavior can be established if a single aspect of bird behavior is assumed operative: when hunting, the grackle relies only on its vision. Given this, it follows that a bird would more readily detect a large larva inhabiting the middle portion of Callie giant bermudagrass canopy (a region where most of the vegetation is green rather than brown, and the predominantly brown markings of M. latipes larvae are less effective as a cryptic device) than it would a small larva. Alternatively, large larvae that were immobile and

Figure 10. Photophase resting position of sixth instar M. latipes larva in Callie giant bermudagrass, C. dactylon. Photograph taken at 16:30 hrs.

closely appressed to the brown stems and leaf sheaths found near the soil surface (Fig. 10) would be more likely to go unnoticed by the larvae-hunting birds. Thus, a plausible explanation for the earlier downward movements (that contribute to the lessened slope of the model's decending phase) of the fifth and sixth instar larvae is that this behavior is a response to selection pressure exerted by avian predators, and that those large larvae that return to the lower portion of the grass canopy before the birds arrive are more likely to reach maturation.

Finally, the data presented in Figure 9 may prove useful in designing a sampling program that focuses on behavioral characteristics of third and fourth instar larvae. Examination of these data indicates that the larvae of this age group are most mobile during the intervals 18:30 hrs to 20:30 hrs and 07:00 hrs to 08:00 hrs. If a larva in motion is more readily dislodged from grass foliage than a larva at rest, and the sampling method employed relies on larval dislodgement; then sampling conducted at these two times can be expected to yield a higher proportion of an existing larval population than would comparable efforts conducted at other times.

Evaluation of a Grassland Sampling Device

Preliminary tests revealed several noteworthy points. First, the rake head worsened machine performance; when set for either 5 or 10 cm tine spacings, attachment of the rake head caused the sampler's forward progress through the

Figure 11. Behavior of M. latipes larvae in the pushcart sampler's cage.

Callie giant bermudagrass to proceed so jerkily that larvae trapped by the cage were often bounced out. Second, larval catch was inversely proportional to cage ground clearance setting, with virtually no larval capture occurring when the ground clearance was set at 15 cm. Third, examination of the cage floor immediately following a sample trial showed that the vast majority of larvae captured were lying on the anterior one-fifth of the floor's surface, and that within less than a minute most of these larvae had uncurled and were crawling about on the screen floor. Captured larvae were often seen to move toward the cage's open front; however, upon encountering the ca. 2 cm wide aluminum frame, these larvae were invariably seen to "rear-up" as if in search of some structure upon which to climb. Upon finding nothing there, larvae so engaged usually redirected their movements and proceeded toward the cage's walls (rarely, toward the interior). Finally, captured larvae evinced a pronounced negative geotaxis. Within five minutes after their capture, virtually all larvae in the cage had moved to the cage walls, climbed half of the cage height (ca. 25 cm), and had come to rest oriented such that their head capsules were uppermost (Fig. 11).

Analysis of the counts that were made immediately prior to tests of sampler efficacy revealed that the number of marked larvae present in each 1 m^2 plot declined through time (Table 12). Daylight inspections revealed that the soil surface in each plot bore numerous bird tracks and a

Table 12. Attrition of marked M. latipes larvae in plots[a] of Callie giant bermudagrass, C. dactylon.

Hours elapsed since release[b]	Mean[c] number of marked larvae present per treatment[d]				
	A	B	C	D	Total[e]
9	30.0	30.0	30.0	30.0	30.0
22	17.0	15.8	10.4	10.0	13.3
33	4.4	8.6	5.8	5.4	6.0
46	1.8	7.0	1.2	3.8	3.5
57	1.2	2.6	0.4	2.2	1.6
70	0.6	1.2	0.0	1.0	0.7

[a] Rectangular (0.5 m x 2.0 m) field plantings containing 24-day-old grass.

[b] Marked larvae initially released at 22:00 hrs.

[c] Means are each of r=5 replications per treatment per time; each replication initially contained m=30 marked larvae.

[d] Treatments A, B, C, and D consisted of an application of Dayglo® fluorescent pigment No. 15, 16, 18, and 21, respectively.

[e] Mean number of larvae observed per time on an experiment-wide basis; each mean is of n=20 observations.

Table 13. Summary statistics of the proportion of marked *M. latipes* larvae present per plot recaptured per trial by the pushcart sampling device. Data of trials conducted at two different times.

Recapture conducted at 9 hours post-release:

Treatment[a]	Mean[b]	Std.Err.	Precision[c]	Time
A	0.0733	0.0125	17.01	07:00
B	0.0933	0.0245	26.23	07:00
C	0.0667	0.0183	27.38	07:00
D	0.0800	0.0170	21.23	07:00
Total	0.0783	0.0081	11.25	07:00

Recapture conducted at 22 hours post-release:

Treatment[a]	Mean[b]	Std.Err.	Precision[c]	Time
A	0.1263	0.0163	12.89	20:00
B	0.0762	0.0226	29.61	20:00
C	0.1104	0.0235	21.29	20:00
D	0.1603	0.0281	17.53	20:00
Total	0.1183	0.0175	9.94	20:00

[a] Treatments A, B, C, and D consisted of an application of Dayglo® fluorescent pigment No. 15, 16, 18, and 21, respectively in n=5 plots per treatment.

[b] Number of larvae captured divided by the number of larvae present per plot per time.

[c] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

few feathers; thus, bird predation was probably the chief cause of reductions in the number of marked larvae per plot. Due to the magnitude of larval losses, only those data obtained for sampler trials conducted at 9 and 22 hours post-release (these times corresponded to 07:00 and 20:00 hours, respectively) were considered for further analysis.

As evidenced by the comparable magnitudes of the standard errors accompanying the mean proportion of larvae recaptured per treatment, treatment means within times were statistically equivalent (Table 13). This time-specific homogeneity has a twofold importance. First, it is an indication of consistency, as regards both sampler efficacy and larval behavior, from plot to plot per time; and second, it is supportive of comparisons between times being made on the basis of estimates derived from data pooled per time.

A two-tailed, t-test evaluation for the difference between two sample means from populations having different variances revealed that the proportion of marked larvae per plot captured by sampler trials conducted at 20:00 hrs was significantly ($t_{calc} = -2.7197$, $df_{adj} = 35$, $\alpha/2 = .025$) different than the proportion captured at 07:00 hrs. Construction of a 95% confidence interval about the difference yielded 0.0399 ± 0.0288. As indicated by the statistics presented for totals per time (Table 13), the higher proportion was obtained for trials conducted at 20:00 hrs.

Judging from these data, the pushcart sampler yielded only slightly better results at one time than another; more-

over, at even the better of the two times, the device caught only slightly more than 10% of the larvae present. Taken alone, such a finding would seem adequate grounds to dismiss the device as one having little or no potential. Two points argue against such a conclusion. First, the higher level of larval capture occurred at a time (22 hrs post-release) when the average larval populational density was relatively low (i.e., 13.3 larvae per m^2; Table 12). This implies that the sampling device is functional when larval populations are at subinjurious densities. Second, the amount of error term contained in each of the two time-specific estimates of mean larval recapture was quite low (11.25% and 9.94% for total effort at 07:00 and 20:00 hrs, respectively; Table 13). Thus, even though the number of larvae captured per trial was low, results from trial to trial were consistent.

Laboratory Experiments

Chorion Consumption

Single-classification analysis revealed that the M. latipes ova examined were significantly non-uniform (Table 14) in the amount of spheroidal portion of the chorion found consumed by an emerging first instar larva. The logical interpretation is that different larvae consume differing amounts of chorion at (or just after) hatching. If this interpretation is in fact correct, then the findings previously reported by Van Dinther (1954), who maintained that M. latipes larvae eat the chorion, as well as those put forward by Ogunwolu and Habeck (1975), who found the chorion was not consumed by the newly-hatched larva, are both (in some measure) valid claims (q.v., Figure 12).

The seemingly contradictory findings of previous research efforts could have been due to a group-specific (rather than an egg-specific) phenomenon. Although a good starting point, analysis by single classification admits no provision for determination of how much of the observed variability is due to differences among the eggs themselves as opposed to differences that are due to the random effect of an egg having been a member of a particular group. This difficulty is overcome through partition of the variability detected by single classification into component-specific variation; such a partition (via a nested analysis of variance: repeated measures in eggs; eggs within groups) is presented in Table 15.

Figure 12. Differences in the degree of chorion consumed by newly eclosed M. latipes larvae.

Table 14. Single-classification ANOVA of a once-repeated measurement of the chorion consumed by an emerging first instar M. latipes larva.

SOURCE	df	SS	MS	F
Among Eggs	79	344.775	4.364	29.095*
Within Eggs	80	12.000	0.150	
Total	159	356.775		

* F-statistic significant at the $\alpha = .05$ level.

Table 15. Two-level nested ANOVA of the chorion consumed by an emerging first instar M. latipes larva.

SOURCE	df	SS	MS	F
Among Groups[a]	7	49.275	7.039	1.715
Among Eggs within Groups	72	295.500	4.104	27.361*
Error	80	12.000	0.150	
Total	159	356.775		

* F-statistic significant at the $\alpha = .05$ level.

[a] Each group contained n=10 M. latipes ova.

The variability in chorion consumption attributable to differences among the groups proves to be a non-significant contributor to the overall experimental variance (Table 15), a clear indication that the heterogeneity in chorion consumption evidenced among eggs is substantially homogeneous among groups. Such group homogeneity is perhaps better seen in a comparison of the mean consumption values obtained per group; these values, accompanied by their respective standard errors and precisions, are presented in Table 16.

The average consumption value per group, with the exception of group 4, lies between 3.05 and 4.15 (Table 16). The interpretation here is that on the average, somewhere between one-half and two-thirds of the spheriodal portion of a M. latipes ovum is consumed by a newly-eclosed larva. The value reported as a total (an overall mean across groups) corroborates this interpretation. Similarly, values obtained for the standard-error-to-mean-ratios indicate that the proportion of each group mean's contained error is a matter of only a few percent; thus, the degree of precision with which mean chorion consumption is estimated lies well above levels generally conceded as accptable for biological applications (Barfield 1981, Kogan and Pitre 1980, Southwood 1978).

The nested analysis confirms that significant variation in amount of chorion consumed by a first instar larva exists among eggs within groups (Table 15); moreover, judging from the magnitude of the calculated F-statistic, the variability

Table 16. Summary statistics of the amount[a] of chorion consumed by an emerging first instar M. latipes larva.

Group[b]	Mean	Std. Err.	Precision[c]
1	3.05	0.344	11.28
2	3.90	0.239	6.14
3	4.05	0.276	6.82
4	2.40	0.413	17.20
5	3.55	0.285	8.04
6	3.95	0.328	8.31
7	4.15	0.365	8.79
8	3.65	0.254	6.96
Total	3.59	0.118	3.30

[a] Amount determined by inspection at 45X magnification; the portion of the chorion consumed by an eclosing larva was accorded a discrete, scalar, value ranging from 1 to 5.

[b] n=10 M. latipes ova; each ovum measured twice.

[c] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

is substantial. This raises two points. First, it seems clear that the interpretation suggested by the results of the single classification analysis (i.e., different larvae consume differing amounts of the chorion's spheroidal portion) has enhanced credibility. Second, elucidation of the differences in the amount of chorion consumed, in terms of the proportion of eggs in each consumption category, is justified. These data are presented in Table 17.

Slightly less than one-fifth of the eggs examined were in the lowest consumption category; an even lower proportion fit the criterion for inclusion in Category 2 (Table 17). Over three-fourths of the eggs examined had at least one-half of the spheroidal portion of the chorion consumed; and of these, most were (for all practical purposes) completely consumed. Judging from these data, it would appear that newly-eclosed M. latipes larvae more often opt to consume the chorion than to not do so.

Two other features of the data presented in Table 17 merit mention. First, 31.62% of the estimated mean proportion of eggs accorded placement in Category 2 is directly attributable to an error term; at the same time, the error of estimation for the means of the other categories is, in every case, less than 25%. This disjunction (whose cause in fact remains unknown) suggests that the comparative rarity of an egg in Category 2 is being reflected. Second, the kind of change evidenced in the proportion of eggs per category (when viewed from a category-to-category perspective)

Table 17. Point estimates and precisions for the proportion of M. latipes ova observed in each of five different chorion consumption categories.

Category[a]	Mean[b]	Std.Err.	Precision[c]	n[d]	N[e]
1	0.1875	0.0446	23.72	10	16
2	0.0500	0.0158	31.62	10	16
3	0.1313	0.0269	20.54	10	16
4	0.2438	0.0438	17.95	10	16
5	0.3813	0.0526	13.80	10	16

[a] Values indicate the amount of chorion per ovum consumed by a newly-eclosed first instar M. latipes larva, as determined by visual estimation of chorion loss from the spheroidal portion of each ovum; these are defined as follows:
1 - minimal loss, spheroidal portion virtually entire;
2 - ca. 1/3rd of spheroidal portion missing;
3 - ca. 1/2 of spheroidal portion missing;
4 - ca. 2/3rd of speroidal portion missing;
5 - spheroidal portion virtually absent.

[b] Proportion of ova per group.

[c] $(s_{\bar{y}}/\bar{y})$ x 100%.

[d] Number of ova per group.

[e] Number of groups.

suggests the presence of an "on-off" type of larval behavior; moreover, it seems plausible that a "threshold" for chorion consumption lies somewhere between Category 2 and Category 3. Were such to ultimately prove correct, then the seemingly contradictory findings put forth by Van Dinther (1954) and Ogunwolu and Habeck (1975) on the subject of chorion consumption are more easily reconciled.

Finally, since the result of this study indicates most M. latipes larvae consume at least one-half of the chorion, it seems fitting to tender some biologically meaningful mechanism that may help account for this behavior. Conservation of comparatively scarce resources is a likely candidate. The chorion of insect eggs is rich in several compounds (eg., chitin, chorionin, and related glycosaminoglycans) known to be important constituents of insect cuticle (Chippendale 1978). It is not beyond reason to suspect that chorion consumption by a newly-eclosed larva would confer a selective advantage by raising the haemolymph titer of these compounds, and when the onset of cuticle synthesis ensues prior to the next molt, such individuals would have at their disposal both more and cheaper (the requirement of de novo synthesis having been lessened) raw material for resultant new cuticle deposition.

Early-Instar Feeding Surface Preference

Although the larvae employed for this assay eclosed near-simultaneously (±1.5 hours), some variability was evidenced in the amount of time the larvae spent in each stadium. These differences in the age structure (Table 18) of the larvae in any given dish probably had very little impact on data integrity. At the time of en masse transfer, a majority of the larvae were in an advanced premolt (i.e., the head capsule of the previous feeding stage, although still intact, is covering only the mandibular/maxillary area of the newly-formed head capsule) condition; those that were not had either just molted to the succeeding stadium (new head capsule not yet fully tanned), or were in the non-feeding state that signals the the onset of the premolt condition (i.e., newly forming head capsule is prominantly evident and positioned beneath the cervical conjunctiva; larva more or less motionless and somewhat sluggish in its response to disturbance). The number of hours post eclosion that elapsed before the larvae in each petri dish evinced the conditions just described was 69 hours and 108 hours for transition from first instar to second instar, and second instar to third instar, respectively. Specific proportions per condition for the larvae in each petri dish at both of these times are presented in Table 18.

Although the bermudagrass was positioned in the petri dishes to permit larval access to both blade surfaces, none of the grass blades in any of the petri dishes bore the

Table 18. Age structure of M. latipes larvae group-cultured in 150 mm petri dishes supplied with terminal growth of Callie giant bermudagrass, C. dactylon. Data for observations at two different times.

69 Hours Post-eclosion

Petri Dish	No. of Larvae per Stage[a]					
	I	(II)	II	(III)	III	Total
1	---	8	2	---	---	10
2	---	13	---	---	---	13
3	---	8	2	---	---	10
4	1	8	1	---	---	10
5	1	7	2	---	---	10
6	2	5	3	---	---	10

108 Hours Post-eclosion

Petri Dish	No. of Larvae per Stage[a]					
	I	(II)	II	(III)	III	Total
1	---	---	---	10	---	10
2	---	---	1	9	---	9
3	---	---	1	8	1	10
4	---	---	2	8	---	10
5	---	1*	2	7	---	10
6	---	---	3	7	---	10

[a] Roman numerals correspond to larval stadia; parentheses about numerals indicate advanced premolt condition.

* Dead larva; removed after count.

slightest sign of early-instar M. latipes feeding scars on the blades' undersurfaces (Table 19). This high degree of blade-surface specificity suggests that both first and second instar M. latipes larvae strongly prefer to feed on only the upper surface of Callie giant bermudagrass blades.

The mean number of feeding scars per dish incurred by second instar larvae was nearly twice that obtained for dishes of first instars (Table 19). Construction of a 95% confidence interval about the difference between the means determined for the two larval age groups reveals this difference to be 17.33 ± 5.26 scars per dish (adjusted df=8). Such a finding lends credence to an expectation of a twofold increase in larval appetite accompanying the transition from first to second instar. The standard-error-to-mean ratio was substantially less than 25% of the mean's point estimate (Table 19); thus, considerable uniformity in the number of feeding scars per sample unit of 10 larvae was evidenced and n=6 petri dishes was a sample size adequate for meaningful point estimation.

The most striking feature of this study is that even though the larvae had free and equal access to both surfaces of the bermudagrass blades, they (the larvae) categorically rejected the blades' undersurfaces as feeding sites. At the time of their introduction, the larvae were placed (via an artist's brush) onto the moistened filter paper discs that lined each petri dish's bottom. After an initial death-feigning response (larva tightly curled and quiescent, this

Table 19. Summary statistics of the feeding surface preferences of first and second instar M. latipes larvae cultured on Callie giant bermudagrass, C. dactylon, blades.

First Instar Larvae[a]

Surface	Mean[c]	Std.Err.	Precision[d]	Range
Upper	17.167	1.302	7.58	14,23
Lower	0.0	0.0	----	----

Second Instar Larvae[b]

Surface	Mean[c]	Std.Err.	Precision[d]	Range
Upper	34.500	1.875	5.44	31,41
Lower	0.0	0.0	----	----

[a] Developmental period beginning at 3 hours post-eclosion and terminating at 69 hours post-eclosion.

[b] Developmental period beginning at 69 hours post-eclosion and terminating at 108 hours post-eclosion.

[c] Average number of feeding scars per 150 mm petri dish containing the terminal portion of a primary stem of bermudagrass and 10 M. latipes larvae. Means are of n=6 dishes.

[d] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

behavior typically lasted ca. 1 minute and rarely more than 2 minutes), the larvae were seen to uncurl and begin moving about in a seemingly randomly-directed, unceasing, search behavior. At the first instance of the larval head capsule making contact with a grass blade (either upper or lower blade surface), a searching larva would immediately climb onto the blade, move to the blade's margin, and either quickly come to rest or move some distance along the margin (sometimes an entire blade would be traversed) and rest. Blade margins were markedly preferred as resting sites for both first and second instar larvae; however, in a few instances, larvae opted to rest in the curled portion of incompletely opened blades or on a mature blade's upper surface.

Since care had been taken to arrange the grass blades in the petri dishes to permit larval access to both blade surfaces, it seems reasonable to suspect that the larvae were perhaps responding to differences in substrate texture that are consequences of blade morphology.

Scanning electron microscopy reveals the upper and lower surfaces of Callie giant bermudagrass blades to have markedly different textures (Figure 13). This difference is chiefly due to the presence or absence of longitudinally arranged rows of tooth-like trichomes, with these particularly evident along the principal veins and blade margins. On the upper surface of Callie blades, these trichomes are much reduced in both size and number; however, they are much

more evident on a blade's lower surface. Perhaps early-instar M. latipes larvae find the presence of these trichomes sufficently troublesome to deter normal larval feeding activity. For such to be the case would certainly help provide a biological mechanism for explaining the observed differential in larval behavior. Moreover, it is suggestive of a possible plant antiherbivory strategy that might be exploited by a plant breeding program: development of a bermudagrass variety that has tooth-like trichomes on both blade surfaces. Such a variety could prove a substantial impediment to the developmental progress of early-instar M. latipes larvae, either by prolonging the time spent per stadium (desirable both because it would permit a longer detection period during a time of minimal crop damage and because of an increase in the time young larvae would be exposed to natural enemies), or by increasing the likelihood of larval mortality due to inadequate grass consumption. Although the current evidence is mainly circumstantial, one final point merits mention. None of the blades in any of the dishes (containing either first or second instar larvae) bore any evidence of having been notched along their margins. Since 60 larvae were employed in the assay of feeding surface preference, it seems reasonable to conclude that leaf notching (blade consumption from the margin toward the midrib) is an activity not undertaken until at least the third larval stadium is attained. Coincidentally, the tooth-like trichomes referred to above are well represented

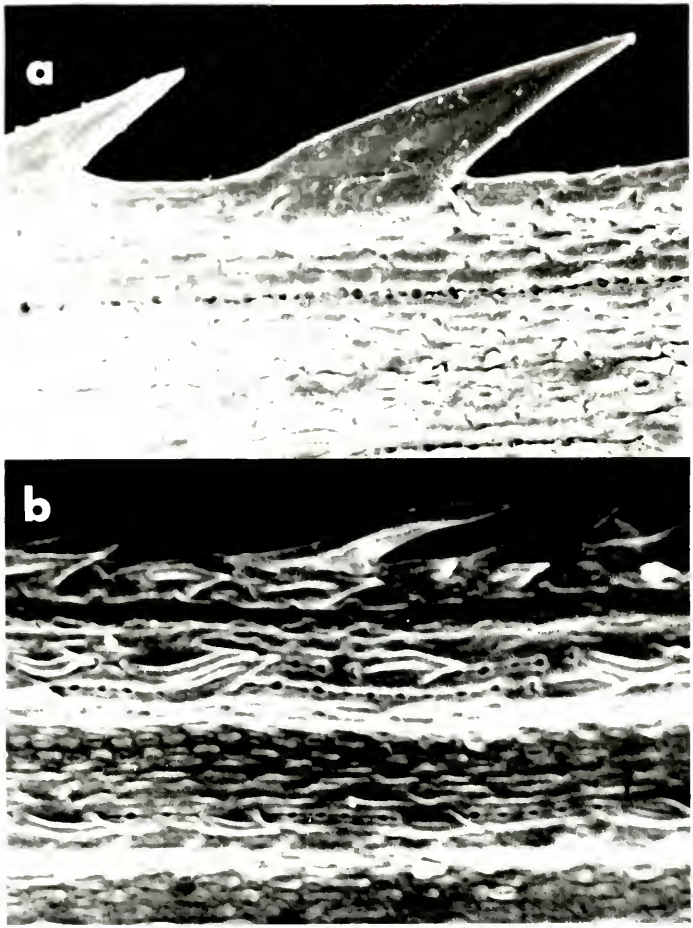

Figure 13. Electron photomicrograph of a Callie giant bermudagrass, C. dactylon, blade.
a) Upper surface; b) Lower surface.

along blade margins. Enter a third circumstance: most of the first and second instar larvae were observed to rest along blade margins. Unification of these three points (the larvae were present but did not feed where the tooth-like trichomes were abundant) seems to underscore the role of the trichomes in an antiherbivory mechanism.

Stage-Specific Developmental Time

The characterization of holometabolous development incorporates the idea of complete transformation of form with that of distinct separation of successive developmental stages (Torre-Bueno 1978). Undoubtedly, the numbers of those who would endorse such a definition are legion; and rightfully so, for little effort is required to see its utility, especially in the study of insect morphology. The notion of "distinct separation" becomes a principal focal point when the elucidation of stage-specific developmental time is the stated experimental objective. A compound difficulty arises. Both time and developmental progress can be thought of as continua (a perspective readily acquired after having once observed a larva making the transition from one stadium to the next, which in the case of M. latipes may require more than half of a day) whose partitionings are artificial (and so, a source of error). However, errors of this kind (judgemental errors) seem small when compared with those arising from interaction of the time continuum, the biological continuum, and the monitor interval (i.e., the time elapsing between successive viewings of the subjects).

Table 20. Summary statistics for the "error intervals"[a] accompanying the stage-specific developmental times of *M. latipes* reared in the laboratory on *C. dactylon*.

Interval[b]	Mean[c]	Std. Err.	Precision[d]	n[e]
EC → I	2.74	0.111	4.06	38
I → II	12.18	0.216	1.77	38
II → III	8.32	0.520	6.25	38
III → IV	7.31	1.279	17.48	38
IV → V	10.45	0.806	7.71	38
V → VI	15.06	1.056	7.02	35
VI → PP	15.13	0.394	2.60	38
PP → P	12.26	0.847	6.86	38
P → A	6.35	0.712	11.20	36
Overall	9.94	0.325	3.27	337

[a] Time elapsed between the last recorded instance of seeing an individual in a given developmental stage and the first recorded instance of seeing the same individual in the succeeding stage.

[b] Roman numerals indicate larval stadia; Capital letters indicate eclosion, prepupal, pupal, and adult stages.

[c] Elapsed hours.

[d] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

[e] Number of individuals observed per interval.

The most modest experience in the laboratory culture of insects (and probably most other organisms) brings with it a hearty appreciation of a simple truth: the insects being cultured have no propensity to modify their developmental progress to suit the scheduling whims of the investigator. Moreover, the ready solution (continuous monitoring) is apt to prove impracticable. The recourse is compromise, and the consequence is no trivial matter: error that admits no partition even though component sources are recognized.

Although composite from the standpoint of source, such error is specific in time; for it corresponds to a discrete interval of the biological continuum; and hence is, in every instance of its appearance, quantifiable. These data, as they apply to the successive stages of M. latipes' developmental time, are presented in Table 20. Their importance is threefold. First, they contribute substantially to the establishment of the dimensions of each transition interval (for example, hatch of the 38 incubated eggs occurred during a ca. 3 hour period; Table 20). Secondly, since neither the means nor their determined precisions are constant values, these data demonstrate that the monitor interval was not held constant for the entire developmental period (when examination of the petri dishes revealed that most of the subjects could be expected to change from one stadium to another in the next few hours, the monitor interval was reduced). Finally, and perhaps most importantly, these data provide a good indication of both the precision that can be

Table 21. Summary statistics for stage-specific developmental times of M. latipes reared in the laboratory on Callie giant bermudagrass, C. dactylon.

Stage[a]	Mean[b]	Std. Err.	Precision[c]	n[d]
I	96.53	0.222	00.01	38
II	175.89	1.022	00.06	38
III	218.79	1.091	00.05	38
IV	270.97	1.373	00.51	38
V	336.63	2.899	00.86	38
VI	406.43	2.805	00.69	35
PP	489.82	3.456	00.71	38
P	531.32	3.022	00.57	38
A	740.19	2.938	00.40	37

[a] Roman numerals indicate larval stadia; capital letters indicate prepupal, pupal, and adult stages.

[b] Elapsed post-ovipositional hours for first detection.

[c] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

[d] Number of observations per stage.

expected from a sample size of n≈35 M. latipes larvae and the magnitude of the overall error term (ca. 10 hours) that should accompany any estimate of stage-specific development when the methodology applicable to this experiment is used.

Point estimates of the number of hours elapsed from the first detection of ova to the first detection of each developmental stage are presented in Table 21. Two points merit mention. The standard error accompanying each of the means gains magnitude as developmental progress increases. This is an indication that variability in developmental time (as measured among individuals per specific time) is at least in part a function of organism age; moreover, the relationship between the two is one of direct proportion. Secondly, the precision with which each mean is estimated seems "too good to be true"; however, it must be remembered that the better measure of error lies in the estimation of the transitional intervals (see Table 20). Thus, the high level of precision found to accompany the means presented in Table 21 is not specious per se, but rather serves to illustrate that the error remaining (after transitional interval error has been accounted for) is only a small portion of the total error term. In fact, the high level of precision proves to be a most useful feature, for it establishes a framework within which stage-specific developmental durations may be derived: finding the difference between any two successive stages' mean elapsed time to first detection. These are presented in Table 22.

Table 22. Stage-specific partition of derived[a] developmental duration for M. latipes reared in the laboratory on Callie giant bermudagrass, C. dactylon.

	Duration			
Stage[b]	Hours	Days	Range (days)	% Total
Egg	96.53	4.02	3.6 , 4.4	13.04
I	79.37	3.31	2.9 , 3.7	10.72
II	42.89	1.79	1.4 , 2.2	5.79
III	52.19	2.17	1.8 , 2.6	7.05
IV	65.67	2.74	2.3 , 3.1	8.87
V	69.80	2.91	2.5 , 3.4	9.43
VI	83.39	3.48	3.1 , 3.9	11.27
PP	41.50	1.73	1.3 , 2.1	5.60
P	208.87	8.70	8.3 , 9.1	28.22
Total[c]	740.19	30.84	29.7 ,32.5	100.00

[a] The difference between the mean number of hours elapsed before first observing a given developmental stage and the mean number of hours elapsed before first observing the next succeeding developmental stage.

[b] Roman numerals indicate larval stadia; capital letters indicate prepupal and pupal stages.

[c] Time elapsed from oviposition to adult emergence.

The amount of time M. latipes spends per developmental stage varies broadly when different developmental stages are contrasted each with the other (Table 22). The duration of the prepupal period and that of the second larval stadium approached equivalency and so vied for the distinction of being shortest; pupal duration (being more than twice that determined for any other stage) was clearly the longest. In general, good agreement exists between the findings reported here (especially as regards overall developmental time) and those that have been put forward by others (Ogunwolu and Habeck 1975, Reinert 1975, Vickery 1924); however, with the exception of Reinert (1975), these researchers did not investigate developmental duration on a per stadium basis.

The durations per larval stadium presented in Table 22 differ substantially from those reported by Reinert (1975). For example, he (Reinert) found fifth and sixth instar M. latipes larvae fed Stenotaphrum secundatum (Walt.) Kuntz foliage needed an average of 3.5 and 7.0 days, respectively, for completion of these two stadia (in contrast, the data presented in Table 22 for these two stadia are 2.91 and 3.48 days, respectively). After culturing M. latipes larvae on 5 different diets, Ogunwolu and Habeck (1975) concluded that dietary composition may substantially alter M. latipes developmental time; the disjunction evidenced (especially for the sixth larval stadium's developmental duration) between the data reported by Reinert (1975) and those given here (Table 22) corroborates their findings.

Table 23. Summary statistics of gender-specific pupal masses obtained for M. latipes reared in the laboratory on Callie giant bermudagrass, C. dactylon, blades.

Gender	Mean[a,b]	Std. Err.[c]	Precision[d]	n
Male	0.312e	5.621	1.80	13
Female	0.297e	5.588	1.88	24
Both	0.302	4.247	1.41	37

[a] Pupal mass in grams.

[b] Means followed by same letter not significantly different at the $\alpha = .05$ level.

[c] Values presented are to be multiplied by 10^{-3}.

[d] $(s_{\bar{y}}/\bar{y}) \times 100\%$.

An unequal sample size, pairwise, t-test comparison of male versus female M. latipes pupae obtained from larvae that had been cultured on Callie giant bermudagrass revealed that pupal masses were not significantly different for the two groups (Table 23). Interestingly, however, the average mass determined for these M. latipes pupae was noticeably greater than those that have been reported previously (Reinert 1975, Ogunwolu and Habeck 1975). If resultant pupal mass is a criterion for determining host plant preference, then it would seem that Callie giant bermudagrass, Cynodon dactylon (L.) Pers., is more preferred than either St. Augustinegrass, Stenotaphrum secundatum (Walt.) Kuntz; corn, Zea mays L.; Guineagrass, Panicum maximum Jacq.; or wheat, Triticum aestivum (L.).

CONCLUSIONS

Florida lands producing Pensacola bahiagrass, P. notatum, may be facilitating seasonally-mediated migratory movements of M. latipes adults. The high degree of time specificity evidenced for moth visitations to the racemes of this grass, in conjunction with the moths' propensity to select this grass in lieu of others, enhances the feasibility of utilizing stands of P. notatum as sites for both early detection and quantification of adult M. latipes populations. Moth counts conducted during the interval 21:00 hrs through 23:00 hrs will likely yield reliable estimates.

In stands of Callie giant bermudagrass, C. dactylon, grass age strongly influences moth behavior. Adult M. latipes seem more inclined to rest, mate, and oviposit in stands that possess closed canopies than in those that lack growth dense enough to obscure the soil surface. In consequence, field scouting/sampling efforts aimed at adults in Callie giant bermudagrass fields containing above ground plant growth less than 3 weeks old will likely be of marginal value.

Since moths engaged in ovipositional activities flew and hovered in the interstices of the middle and lower portions of the grass canopy, and seemed equally prone to

deposit their eggs on grass stems, sheaths, ligules and on both the upper and lower surfaces of blades; it would seem that the findings put forward by Fennah (1947) do not apply as an apt description of M. latipes' ovipositional behavior in Callie giant bermudagrass.

Taken in combination, the sessile character, high visibility, and time specificity associated with M. latipes' mating behavior offers promise to the future implementation of nocturnal field scouting as a means for assessing moth populations. However, if pheromone-baited traps are to be the basis of a monitoring program, trap catches obtained between 21:00 hrs and 04:00 hrs will likely yield data that substantially underestimate actual population intensity.

Perhaps as a foreshadowing of the nocturnal behavior demonstrated by the imago, third and older instar M. latipes larvae conduct most of their activities at night. However, fifth and sixth instar larvae function on a timetable different than third and fourth instars. Differences observed in the times at which larvae of these two groups both ascend from protected areas in the lowest portions of Callie giant bermudagrass canopy and return to them are probably consequences that ensue from age-specific differences in efficiency of food conversion, hunger, and likelihood of being detected by avian predators. If a larva in motion is more readily dislodged from grass foliage than a larva at rest, and the sampling method chosen relies on larval dislodgement, then samples taken during either the

interval from 06:00 hrs to 08:00 hrs or from 19:00 hrs to 21:00 hrs are likely to yield a higher proportion of an existing larval population than comparable efforts conducted at other times.

As currently configured, the pushcart sampling device is inadequate for making absolute density estimates of M. latipes larval populations. Its principal shortcomings are twofold: it fails to capture at least 85% of the larvae present, and lacks secondary foliage agitation capability. The degree of consistency evidenced in the evaluative data indicates that this device, if modified, merits further consideration.

Immediately following hatch, M. latipes larvae can be expected to consume more than one-half of the chorion's spheroidal portion. Since the chorion is rich in compounds known to be important constituents of insect cuticle, it seems likely that this behavior is a means by which young larvae avail themselves of materials valuable for subsequent cuticle formation.

If provided equal access to both surfaces of Callie giant bermudagrass blades, both first and second instar M. latipes larvae will feed on only the upper surfaces. The profuse growth of tooth-like trichomes on the lower surfaces and blade margins apparently deters early-instar M. latipes larvae from feeding at these sites. A plant breeding program that culminated in the release of a bermudagrass variety whose blades possessed comparable amounts of these

trichomes on both blade surfaces would likely prove of substantial worth to the forage production community.

M. latipes larvae reared on Callie giant bermudagrass foliage evinced stage-specific developmental times comparable to those previously reported when other grasses were supplied as diet; however, the average mass of the resultant pupae was noticeably greater. If pupal mass is a criterion for determining host preference, then Callie giant bermudagrass is more preferred than St. Augustinegrass, maize, Guineagrass, or wheat.

Viewed in composite, the findings set forth above provide a clearer comprehension of this moth's activities in Florida grasslands. However, several issues require both address and reconciliation before the full potential of these data can be realized by the agricultural community. These include isolation and synthesis of M. latipes' sex pheromone, with subsequent examination of its applicability as a monitoring tool; field studies of moth oviposition preference in different forage grasses; characterization of the heirarchial relation of M. latipes to the other pest lepidopteran species known to inhabit Florida's grasslands; the impact of grass-legume associations on M. latipes populations; and, robust documentation of stage-specific M. latipes damage in forage grasses under field conditions.

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The author was born 31 December 1949 in Gainesville, Florida.

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He has had the privilege of assisting various research projects including pheromone bioassay (corn earworm), moth flight behavior (tobacco hornworm), the impact of thrips in lupine, seasonal presence of fall armyworm in North Florida and southern Georgia, and a state-wide survey of Florida's forage-inhabiting insects.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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August 1985

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